University of Alberta

Anatomy and systematics of North American tylosaurine mosasaurs

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Systematics and Evolution

Department of Biological Sciences

Edmonton, Alberta
Fall 2006

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Your file Votre référence
ISBN: 978-0-494-22235-5
Our file Notre référence
ISBN: 978-0-494-22235-5

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ABSTRACT

The type and associated materials of *Hainosaurus pembinensis* (Reptilia: Squamata) from the Middle Campanian Pembina Member of the Pierre Shale, Manitoba, are redescribed. The anatomy of this species is clarified with comparison to *Hainosaurus bernardi* from the Early Maastrichtian of Belgium, and *Hainosaurus pembinensis* is referred to the genus *Tylosaurus*. A new species of tylosaurine mosasaur, *Tylosaurus saskatchewanensis*, is described from the Late Campanian Bearpaw Formation of Saskatchewan. This species represents the youngest occurrence of *Tylosaurus*. The phylogeny of the mosasaur Subfamily Tylosaurinae is the focus of a cladistic analysis of mosasauroids, expanding the work of previous authors to include *Hainosaurus bernardi*, *Taniwhasaurus oweni*, *Tylosaurus pembinensis* and *Tylosaurus saskatchewanensis*. The findings are consistent with previous studies, and show that *Hainosaurus bernardi* and *Taniwhasaurus oweni* are the most basal tylosaurines, with the species of *Tylosaurus* forming a monophyletic clade.

ACKNOWLEDGEMENT

My supervisor, Dr. Michael Caldwell, provided the opportunity to conduct this research, and the assistance that allowed me to finish it. I benefited greatly from the academic support and friendship of Lisa Budney, Alex Dutchak, Stephanie Pierce, and the other students in the Laboratory for Vertebrate Palaeontology at the University of Alberta. I am grateful to my committee members, Dr. Brian Chatterton and Dr. Mark Wilson, for their assistance during the completion of this thesis and also for their patience!

I am deeply indebted to Mike Waddell and the staff of the Morden Museum for their hospitality during my stay in Morden, for the chance to study the many mosasaur specimens in their collection, and for the permission to borrow many of the quadrates of *Tylosaurus pembinensis*. Gilles Danis and the staff of Prehistoric Animal Structures in East Coulee, Alberta, allowed me access to MDM M74.06.06 in their workshop, and very generously produced plaster casts of the most important elements of this specimen. Jim Woods of the Miami Museum arranged for access to MT 2, and John Andrews shared his knowledge of the specimen. Dr. Graham Young of the Manitoba Museum arranged for access to MM V95.

Dr. Harold Bryant of the Royal Saskatchewan arranged for my access to RSM P 2588.1, and I am very grateful to him for the opportunity to study this beautiful specimen, for his hospitality during my stay in Regina and in subsequent summers, and for the permission to borrow the skull during my research.

The Natural Science and Engineering Research Council of Canada provided funding for much of the research in this project.

Finally, I would like to acknowledge my family and friends: to my father, for assisting me with my research in Manitoba, and for being my biggest fan; to my mother, for always understanding; to my brother Daniel, for his incisive wit and boundless energy; to my sister Hana, for sharing a love of living things; to Jeff Berger, John Cotton, Scott Deederly, Bryce Kelly, Melissa Kennedy, Kris McNutt, Chris Oates, Chantelle Opyr, Norman Poon, Andrea Quint, Kevin Schostek, Jeff Seigel, Paul Shepherd, Zach Sonnleitner, Ted Stewart, Parker Wells, and everyone else at Lister Hall, for their friendship and for welcoming me into a new and strange city; to Alberto De Leon, Nilay Ertemur, Kowlasar Misir, Karen Okamoto, Wolfgang Pfeiffer, Christie Schmelzle, Stephanie Taieb, and the other members of the International Club, for proving that friendship knows no boundaries of distance or language; to Tom Cockburn, Ray Graham, Joe Haegert, Thor Henrich, Marji Johns, Roy and Karen Leeson, Lois Walker, and my other colleagues in the Victoria Palaeontology Society, for fostering a young fossil collector's dreams, and encouraging me at every step; to Justin Ankenmann, Jeremy Harper, Chris Malcolm, and Mike Werner, for putting up with me longer than anyone has a right to; and to everyone else, I haven't forgotten about you!

I dedicate this thesis to my family.

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Chapter 1. Introduction

Mosasaurs are large, predatory marine lizards that appear in the fossil record in the Turonian and go extinct with the closing of the Cretaceous. Skin impressions (Williston, 1898) show that they were scaled like lizards and snakes, and it is to the scaled reptiles, the Squamata, that mosasaurs are most closely related amongst living organisms. In general form they resemble many modern lizards, with an elongate body and a tail that is significantly longer than the torso. The head is comparatively larger, however, and distinctly tapered toward the snout (Fig. 1-1). The lower jaw is robust, and articulated at its midpoint (Fig. 1-2). Of all the bones of the skull, the quadrate, joining the upper and lower jaws, is the most variable and diagnostic (Fig. 1-3). The limbs are comparatively smaller than those of terrestrial lizards, with spreading fingers that formed a paddle (Fig. 1-4). They were fully aquatic, and must have spent their entire lives at sea. During their comparatively brief geological time span, mosasaurs were extremely successful, giving rise to a diversity of genera and obtaining a world-wide distribution.

This introductory chapter begins with an abbreviated history of mosasaur research, describing the most important discoveries and the palaeontologists who made them. The remainder of the chapter prefaces more specifically the studies that make up this thesis, and background knowledge is provided for each of the research chapters that follows. This includes introductions to the tylosaurine mosasaurs, the Western Interior Seaway, where the mosasaurs described in this thesis lived, the Pierre Shale in southern Manitoba, the Bearpaw formation in Saskatchewan, and finally the phylogeny of mosasaurs. The chapter's appendix includes a lengthy, but still incomplete, summary of the skeletal anatomy of mosasaurs, which is intended to provide a comparative context for the anatomical discussions in later chapters.

A Brief History of Mosasaur Research

The recorded history of mosasaurs begins with the apocryphal story of the first mosasaur discovery, as related by Faujas Saint-Fond (Williston, 1898:84-85). A large fossil skull was discovered by labourers in an underground limestone quarry beneath Mount St. Peter, near the city of Maastricht in the Netherlands. A local surgeon, Dr. Hoffman, was an amateur palaeontologist and agreed to pay them for the recovery of the specimen. Upon hearing of this amazing discovery, the owner of the land under which the skull had been found, a clergyman named Canon Goddin, took Hoffman to court over possession of the fossil. Goddin was ultimately victorious and had the fossil moved to his home on Mount St. Peter. The fame of this dramatic fossil soon spread far and wide, and when Napoleon's troops invaded and laid siege to Fort St. Peter, the French general ordered his cannons to avoid hitting Goddin's home. Goddin had already taken measures to ensure the safety of his specimen, however, and the skull was removed to a hiding place in Maastricht. When the French captured the city a reward of 600 bottles of wine was offered for its recovery, and the next day the fossil was triumphantly produced by a group of legionnaires. The skull was shipped to Paris, and it remains in the Museum of Natural History to this day.

It is likely that this tale is not a true history of the skull, fabricated with the aim of justifying the French claim to the specimen, nor is the Paris skull the first mosasaur fossil to have been discovered—that honour goes to another partial skull discovered near Maastricht in 1766 (Mulder, 2003). It was, however, the first mosasaur to be described in a scientific fashion, when Baron Georges Cuvier published on the specimen in 1808.

Fourteen years later Conybeare (1822) finally named it *Mosasaurus*; "*Mosa*" after the river Meuse which flows through Maastricht and "*saurus*" for lizard. He did not designate a species, however, and subsequent authors used the names *M. belgicus*, *M. camperi*, *M. giganteus*, and *M. hoffmanni* for the specimen. The matter was closed when Camp (1942) reviewed the confusing early literature and decided that *Mosasaurus hoffmanni* Mantell, 1829 was the first specific epithet to be applied to the specimen.

The first mosasaur discoveries in the Americas were fragmentary and scattered remains from New Jersey and the Gulf states. The discovery of a nearly complete skull with much of the vertebral column and pectoral girdle on the Missouri River was a notable exception. The anterior end of the snout was collected separately and named *Ichthyosaurus missouriensis* by Harlan (1834). The remainder of the specimen was later described by Goldfuss (1845) as *Mosasaurus maximiliani*. Subsequent authors, such as Camp (1942), correctly noted that the fragment figured by Harlan would fit perfectly onto Goldfuss' skull, making *M. maximiliani* a junior synonym of *M. missouriensis* (Caldwell and Bell, 2005).

Mosasaur research exploded with increased scientific activity in the American West. Both O. C. Marsh and E. D. Cope led field parties into the Niobrara Chalk of Kansas in 1870-1871 and returned with new mosasaur material. After a series of publications from both authors, far too many genera and species were created than the material warranted. Cope and Marsh ended up creating their own names for the same animals, but Cope's appelations have retained priority in all cases save that of *Halisaurus* and *Tylosaurus*. Marsh's best contribution was in 1872 when he accurately diagnosed, though under his own names, the three common Niobrara genera, *Clidastes*, *Platecarpus*, and *Tylosaurus*. Cope's 1875 "Vertebrata of the Cretaceous Formations of the West" was the finest review of mosasaur anatomy to date, and included figures of his important type material.

While American research was still underway, reports of new mosasaurs continued from more distant locations. James Hector (1874) named two new mosasaurs from the Campanian-Maastrichtian of New Zealand: *Leiodon* (=*Liodon*) *haumuriensis* and *Taniwhasaurus oweni*. In Europe, Louis Dollo (1882, 1888, 1889a, 1889b, 1890, 1894) named several new genera from Belgium, including *Plioplatecarpus*, *Prognathodon*, *Phosphorosaurus*, and *Hainosaurus*. French contributions came in the form of *Mosasaurus gaudryi* and *Platecarpus somenensis* (Thévenin, 1896), and new species of *Liodon* (Gaudry, 1892). Merriam's (1894) dissertation in Munich described several new forms from the Kansas Niobrara, including a second species of *Halisaurus*, two new species of *Platecarpus*, and a new species of *Clidastes*.

It was around the turn of the century that more comprehensive ideas about the anatomy and systematics of mosasaurs began to take form. Samuel Williston (1898) provided an excellent review of mosasaur knowledge, describing each of the known skeletal elements and comparing them between taxa, and established the classification of mosasaurs that is still in use today. The next review of this kind was Russell's (1967) classic work, which is still the most important single reference on mosasaur anatomy. Russell made sense of the profusion of genera and species by synonymising many taxa, and provided the first comprehensive mosasaur phylogeny.

Additions to mosasaur knowledge have continued from all over the globe. Accounts of mosasaurs from Niger began with Swinton (1930), who based a new species of *Mosasaurus* on fragmentary remains from Maastrichtian rocks, though this material was later referred to the new genus *Goronyosaurus* by Azzaroli et al. (1972). The Dukamje Formation of southwestern Niger is now thought to contain as many as seven mosasaur genera, an incredible diversity that rivals that of the Niobrara Formation (Lingham-Soliar, 1991). Much older mosasaurs were reported from Turonian rocks of Angola by Telles-Antunes (1964), including *Mosasaurus imbeensis* and the new genus *Angolosaurus*. Wright and Shannon (1988) named a new genus related to *Platecarpus*, *Selmasaurus*, from Alabama. Wiffen (1980, 1990) described further mosasaurs from New Zealand, including *Mosasaurus mangahouangae*, *M. flemingi*, and *Rikisaurus tehoensis*. Dortangs et al. (2002) have reported on a new species of *Prognathodon*, *P. saturator*, from the Maastricht area near the locality where *Mosasaurus hoffmanni* was first collected. Mosasaurs are now known as fragmentary remains from Japan (Suzuki, 1985; Chitoku, 1994) and even Antarctica (Gasparini and del Valle, 1984; Novas et al., 2002).

Many authors have also turned to the very necessary task of re-examining and reinterpreting old collections. Welles and Gregg (1971) reviewed Hector's earlier descriptions, assigning *"Leiodon" haumuriensis* to *Tylosaurus*, removing some of the type material of *Taniwhasaurus* to a new species, *Mosasaurus mokoroa*, and referring *Taniwhasaurus* to the tylosaurines, as well as naming *Prognathodon waiparaensis* from new specimens. In a series of papers, Lingham-Soliar reviewed the anatomy and taxonomy of several European mosasaurs, including *Hainosaurus*, *Leiodon*, *Mosasaurus*, *Plioplatecarpus* and *Prognathodon* (Lingham-Soliar, 1992a, 1993, 1995, 1994a; Lingham-Soliar and Nolf, 1989), as well as the African forms *Goronyosaurus* and

Angolosaurus (Lingham-Soliar, 1988, 1991, 1994b). Caldwell et al. (2005) have revisited Hector's mosasaur material, and synonymised *Tylosaurus haumuriensis* with *Taniwhasaurus oweni*.

Introduction to Tylosaurine Mosasaur Research

The early taxonomic history of the genus *Tylosaurus* is one of the most convoluted in the mosasaur literature. Like many other genera, this history originates from the famous scientific rivalry between Edward Drinker Cope and Othniel Charles Marsh. Cope (1869) placed a fragmentary muzzle, the first mosasaur discovered in Kansas, into *Macrosaurus* Owen, 1849, naming it *Macrosaurus proriger*. One year later he referred the species to Owen's *Liodon* (Cope, 1869-1870), and reclassified *Liodon* to include some other North American species. Marsh (1872a), relying upon large collections of mosasaurs from the Midwest, was quick to identify the many errors and uncertainties in Cope's understanding. He proposed the name *Rhinosaurus* (which was preoccupied by a lizard) for Cope's *Liodon*, and referred all Cope's species to this new genus. Cope (1872) maintained that *Rhinosaurus* was the same as *Liodon*, but suggested the name *Rhamphosaurus* (which was also preoccupied by a lizard) should they not be synonymous. Marsh (1872b) got the final word when he noted the preoccupation of both names, and replaced both *Rhinosaurus* and *Rhamphosaurus* with *Tylosaurus*. This new name was accepted by all subsequent workers, save Cope himself.

Tylosaurus is now one of the best understood of all mosasaur genera, thanks to hundreds of skeletons collected from the Niobrara Formation of Kansas, including a spectacularly complete example that preserves many of the cartilaginous elements

(Osborn, 1899). There are currently three species recognised from the Niobrara Formation: *T. proriger*, *T. nepaeolicus*, and *T. kansasensis* (Everhart, 2005b). *Tylosaurus nepaeolicus* and *T. kansasensis* occur only in the lower Smoky Hill Chalk Member of the Niobrara Formation (Late Coniacian to Early Santonian in age), while *T. proriger* ranges upward from the lower Smoky Hill Chalk into the overlying Pierre Shale (Early Santonian to Early Campanian) (Everhart, 2001).

Specimens of *Tylosaurus* were distinctive in the early mosasaur collections because of an edentulous rostrum on the premaxilla; in *T. nepaeolicus* this rostrum is generally shorter and more rounded (Fig. 1-5), while in *T. kansasensis* and *T. proriger* it is robust and rectangular in outline. In *T. kansasensis* and *T. nepaeolicus* the external nares begin above the midpoint between the third and fourth maxillary tooth, whereas in *T. proriger* this occurs above or slightly behind the fourth maxillary tooth. The parietal foramen of *T. nepaeolicus* is separated from the fronto-parietal suture by 3-4 foramen lengths, in *T. proriger* it is about one length behind the suture, and in *T. kansasensis* it is very close to the suture. The quadrates of these three species are distinct also: in *T. kansasensis* and *T. nepaeolicus* the infrastapedial process is small and low, and the tympanic rim terminates near the ventral condyle (Fig. 1-3C), while in *T. proriger* the rim continues dorsally to terminate on the lateral face of a larger, triangular infrastapedial process (Fig. 1-3D).

United with *Tylosaurus* in the Subfamily Tylosaurinae is a group of large mosasaurs that also share a toothless premaxillary rostrum. The suprastapedial and infrastapedial processes of tylosaurines are short in comparison to those of *Platecarpus* and *Plioplatecarpus*, never coming close to touching each other. The suprastapedial tapers towards its tip. Expansion of the otosphenoid crest of the prootic to cover much of the opisthotic has now been reported from both *Tylosaurus* (Russell, 1967:36-37) and *Hainosaurus* (Lingham-Soliar, 1992a:178), and may prove to be characteristic of tylosaurines in general. The postcranium is very similar to that of *Platecarpus* and *Plioplatecarpus*: haemal arches are articulated rather than fused and the appendicular skeleton is poorly ossified, the articular surfaces of the limb bones rough and unfinished.

The second tylosaurine discovered was *Hainosaurus*, described by Louis Dollo in a series of papers (Dollo, 1885, 1887, 1889). The type species, *H. bernardi*, is based on a single specimen collected from the Early Maastrichtian Ciply Phosphatic Chalk near Mesvin, Belgium. Though it includes a nearly complete skull (Fig. 1-6) and postcranium, the type is poorly preserved and many osteological features are lost. The quadrate has an unusual morphology: a reduced suprastapedial process, a faint infrastapedial process, and a shallow tympanic ala (Fig. 1-3E). Dollo (1904) later named another species of *Hainosaurus*, *H. lonzeensis*, from an isolated premaxilla and vertebrae. He was quick to notice the similarity of *Hainosaurus* to Marsh's *Tylosaurus*, allying the two genera in his "megarynchous" classification on the basis of the long premaxillary rostrum (Dollo, 1890). Despite adding several new genera of mosasaurs and a host of undiscovered anatomical features, Dollo's accounts were often terse and superficial, and did little to establish *Hainosaurus* other than describing the general characteristics of the genus.

Williston (1897) created the Subfamily Tylosaurinae to include Dollo's megarynchous genera, *Tylosaurus* and *Hainosaurus*, though he later remarked that no definite characteristics existed to separate them, except what might be found in the poorly described appendicular skeleton of *H. bernardi* (Williston, 1898:88). In his classic study of North American mosasaurs, Russell (1967) synonymised many of the *Tylosaurus* species created by Cope and Marsh, recognising only two from the Niobrara Chalk: *T. proriger* and *T. nepaeolicus*. Commenting upon the poor preservation of the type quadrate in *H. bernardi*, Russell suggested that the suprastapedial may have been as large as that of *Tylosaurus* in an undamaged example. He concluded that the only "good character" to distinguish *Hainosaurus* from *Tylosaurus* was the greater number of vertebrae anterior to the chevron-bearing (intermediate) caudals in the former genus (Russell, 1967:176).

A new species of *Tylosaurus*, *T. capensis*, was created by Broom (1912) for a frontal-parietal fragment and some undescribed dentulous jaw fragments from the Cretaceous of "Pondoland" (South Africa). The straight frontal-parietal suture, location of the parietal foramen near the suture, and contact of the prefrontal and postorbitofrontal above the orbits do suggest a similarity with *Tylosaurus*, but it is impossible to be more definite without additional skull or postcranial material.

In their landmark treatment of marine reptiles from New Zealand, Welles and Gregg (1971) referred Hector's "*Leiodon*" *haumuriensis* to *Tylosaurus* on the basis of edentulous rostrum on the premaxilla and dentary, though their reconstruction of the lectotype shows a prefrontal that must have contacted the margin of the external nares (Welles and Gregg, 1971:fig. 27). They recognised that *Taniwhasaurus oweni* was also a tylosaurine, based on postorbitofrontal overlap of the prefrontal above the orbit, but repeated Hector's observation of prefrontal contribution to the external nares. Welles and Gregg suggested that these two New Zealand tylosaurines could be synonymous, but felt that enough differences remained to justify their separation.

In his redescription of *Goronyosaurus*, Lingham-Soliar (1988) suggested that the genus was best referred to the Tylosaurinae based on the morphology of the internarial bar and the length-to-width ratio of the skull. The internarial portion of the premaxilla is distinctively wide in *Tylosaurus* and *Goronyosaurus*, but is triangular at its base in *Goronyosaurus*, and rectangular in *Tylosaurus*. In most other aspects of its skull morphology, *Goronyosaurus* does not resemble *Tylosaurus* any more than other mosasaurs, for example the extremely short narial openings, symmetrically bicarinate tooth crowns, fusion of the pelvic girdle (Azzaroli et al., 1972:401), and most importantly the lack of an edentulous rostrum on the premaxilla and dentary. Without the most distinctive anatomical features of the subfamily, it does not seem justified to include *Goronyosaurus* in the Tylosaurinae, and indeed he did not restate this position when he later revisited the mosasaurs of Niger (Lingham-Soliar, 1991).

The first addition to the fossil record of *Hainosaurus* in over a hundred years was Nicholls' (1988) report of a large tylosaurine, named *Hainosaurus pembinensis*, from the Middle Campanian Pierre Shale of Manitoba. Nicholls was able to glean from Dollo's writings several anatomical features that appeared to unite her new species with *H. bernardi*, including: relatively longer external nares, 30% of total skull length, greater number of vertebrae anterior to the intermediate caudals, greater length of the femur relative to the humerus, and small size of the suprastapedial and infrastapedial processes. Nicholls regarded *H. lonzeensis* as a nomen dubium because none of these features are available to distinguish it from *Tylosaurus*. Relatively longer supratemporal fenestrae, a homodont dentition, and a suprastapedial comparable to that of *Tylosaurus* were specific differences between *H. pembinensis* and *H. bernardi*.

Following Nicholls, Bardet (1990) reassigned *Mosasaurus gaudryi* Thévenin, 1896 to *Hainosaurus* because of its large size, contact of the prefrontal and postorbitofrontal over the orbit (a feature of most mosasaur genera), and relatively elongate external nares. Further, she referred it to *H. bernardi* because of its heterodont dentition, even though the Belgian material of *H. bernardi* occurs in the Early Maastrichtian, while *"M." gaudryi* is known from the late Middle Santonian. An early record of *Hainosaurus* in France suggested to Bardet that the genus had an origin in Europe rather than North America.

Lingham-Soliar (1992a) was the first to attempt a comprehensive study of the Tylosaurines, combining a review of the Belgian material of *H. bernardi*, including the type and a second undescribed specimen, with discussions of *Mosasaurus gaudryi* (Thevenin, 1896), which he agreed should be referred to *Hainosaurus*, and other tylosaurine species from Africa: *Tylosaurus capensis* (Broom, 1912), and *Mosasaurus iembeensis* (Telles-Antunes, 1964), which he assigned to *Tylosaurus*. For students of *Hainosaurus*, his descriptions and figures are a welcome supplement to Dollo's writings, and provide an improved diagnosis for the genus based upon a number of newly recognised anatomical features. These include a unique, intertonguing configuration of the premaxilla-maxilla suture, which he terms "double buttressed," and a prefrontal which enters the posterior margin of the external nares. Lingham-Soliar's (1992a) generic diagnosis did not explicitly mention Nicholls' (1988) characters, though the greater number of precaudal vertebrae is evident from his vertebral formula, and his specific diagnosis includes the greater length of the external nares. He agreed with previous authors that the best feature uniting *H. pembinensis* and *H. bernardi* was still their greater number of 'precaudal' vertebrae, but cast doubt on this relationship by observing that variation in the number of "presacral" vertebrae is not unusual within the same species, and that *H. pembinensis* lacks the diagnostic features mentioned above. Finally, he agreed with Nicholls (1988) that *H. lonzeensis* was not sufficiently different from *H. bernardi* to warrant a new species, but referred it to *Hainosaurus* sp.

In Lindgren and Siverson's (2002) treatment of *Mosasaurus ivoensis* (Persson 1963), they referred the species to *Tylosaurus* and supplemented the isolated tooth crowns of the type with some further tooth, jaw, and vertebral material. Their descriptions of the tooth morphology of tylosaurines are the finest yet published, including firsthand accounts of *H. bernardi*, *H. pembinensis*, and *T. proriger*, as well as *T. ivoensis*. They note dental differences between *H. bernardi* and *T. proriger*: in *Tylosaurus* the tooth crowns are nearly circular in cross section and have enlarged lingual surfaces, while in *Hainosaurus* the crowns are compressed buccolingually and the surfaces are nearly symmetrical, tooth carinae are weak in *Tylosaurus* but pronounced in *Hainosaurus*. In these respects, *H. pembinensis* most resembles *Tylosaurus*. Lindgren and Siverson question other anatomical features described by Nicholls (1988), and propose that these features are also more similar to *Tylosaurus*. They suggest that *H. pembinensis* and *T. ivoensis* may in fact be synonymous, but do not state this formally. Lindgren and Siverson also dispute Lingham-Soliar's (1992a) diagnostic features by noting that a double buttressed premaxillary suture is present in specimens of *Tylosaurus*, and that his reconstruction of *H. bernardi* (Lingham-Soliar, 1992a:fig. 3) makes the external nares look no longer than those of *T. proriger* (Russell, 1967:fig. 92).

Recent years have seen the addition of several tylosaurine species. Novas et al. (2002) have named a new genus from the Late Campanian-Early Maastrichtian Santa Marta Formation of Antarctica, *Lakumasaurus antarcticus*. A series of papers by Everhart has reported on the stratigraphic occurrence of *Tylosaurus* species in the Smoky Hill Chalk of the Niobrara Formation (Everhart, 2001), the morphology of *T. nepaeolicus* (Everhart, 2002), the earliest record of *Tylosaurus* sp., a fragmentary skeleton from the Early Coniacian Fort Hays Limestone of Kansas (Everhart, 2005a), and most recently the naming of a new species of *Tylosaurus* from the Niobrara, *T. kansasensis*, which had been mentioned by Bell (1993, 1997) but never formally described (Everhart, 2005b).

Most recently, Caldwell et al. (2005) have again revisited Hector's New Zealand mosasaurs, confirming the suspicions of Welles and Gregg (1971) and synonymising *Tylosaurus haumuriensis* with *Taniwhasaurus oweni*, the latter having priority, as well as referring some new material to the species. Many features mark it as a tylosaurine, but the prefrontal contribution to the narial margin indicates that the species should not belong in *Tylosaurus*.

Introduction to the Western Interior Seaway

The mosasaurs described in this thesis lived in a shallow epicontinental sea called the Western Interior Seaway that stretched from the Arctic Ocean to the Gulf of Mexico. This sea formed in a foreland basin along the eastern margin of the developing Cordillera, and its history is tied to the tectonic evolution of the continent's western margin (Kauffman and Caldwell, 1993). The western foredeep of the basin had the highest rate of subsidence, and deposition was primarily of coarse-grained terrigenous clastic sediments in a coastal plain to shallow marine setting. Subsidence exceeded sedimentation in the basin's axis, creating a deep trough with thick sequences of medium to fine-grained terrigenous clastics and pelagic carbonates deposited in a deep water setting. The eastern third of the sea formed a shallow, tectonically stable platform with sedimentation of fine-grained terrigenous clastics and pelagic carbonates.

Eustatic fluctuations had a profound impact on the development of the sea. Flooding of the continental craton began from the north as early as the late Berriasian (earliest Cretaceous), and continued progressively southward as eustatic sea level increased, finally connecting with the southern portion of the seaway in the early late Albian (Stelck, 1991). Sea level dropped briefly to isolate the north and south water masses until the late late Albian, but continued to rise thereafter and the seaway remained open until the middle Maastrichtian (Kauffman and Caldwell, 1993). Sea level fluctuations throughout the history of the Western Interior Basin produced a complicated series of transgressive-regressive cycles, or cyclothems (Kauffman, 1977). The longest of these transgressive-regressive events, the Niobrara Cycle, began in the late Turonian and continued to the middle Campanian, creating a lengthy period of flooding during which the extensive chalks of the Niobrara Formation were deposited. A pair of later Campanian cycles, the Claggett and Bearpaw of Kauffman (1977), were shorter and less widespread, but the organic-rich clays and shales of the lower Pierre Shale and Bearpaw Formation were deposited during these cycles, respectively. Maximum flooding of the final cycle occurred in the middle Maastrichtian, and the seaway quickly retreated, disappearing during the late Maastrichtian.

Water conditions in the sea must have varied widely with eustatic perturbations, but watermass models have all struggled to account for long periods of anoxia and organic carbon accumulation on the sea floor (such as the Niobrara Formation). Kauffman (1988) suggested that the normal condition during the seaway's lengthy open phase was a stratified water column of warmer, normal to hypersaline waters from the south overlying colder, slightly brackish waters from the north. This stratification suppressed the downward circulation of oxygenated surface water, leading to periods of anoxic bottom waters and organic carbon deposition. Hay et al. (1993) proposed instead that mixing of north and south water masses at the center of the basin increased their density, creating a zone of downwelling would have carried organic material to the bottom of the water column and consumed the available oxygen. On a smaller scale, zones of upwelling may have brought nutrients to the surface and stimulated local organic production (Parrish and Gautier, 1993). Temporary disruptions of the water stratification, in the form of mixing from large storm events, seem to have been frequent (Ericksen and Slingerland, 1990).

The poorly oxygenated bottom waters of the seaway supported low diversity communities of opportunistic and low-oxygen-adapted molluscs and benthic trace-makers; typical marine groups such as sponges, bryozoans, brachiopods, corals, and echinoderms are absent (Sohl, 1967; Kauffman, 1977). The connection of the seaway in the Albian allowed a northern cool temperate biota to mix with a southern warm temperate-subtropical biota at the centre of the basin (Kauffman, 1984). This zone of mixing was characterised by high endemism, particularly of ammonites (Cobban, 1993). Pelagic vertebrates were more cosmopolitan and tolerant of changing water conditions, and there is little evidence for the complex biogeographic zonation seen in invertebrates (Kauffman, 1984). Nicholls and Russell (1990) suggest a simple bipartite scheme for the biogeography of vertebrates in the Campanian: a northern biotic province with low diversity communities dominated by *Hesperornis*, plesiosaurs, and *Platecarpus*, and a southern biotic province with a high diversity of turtles and sharks, dominated by *Ichthyornis* and *Clidastes*.

Extensive collections of marine invertebrates from the Western Interior Basin have yielded a biostratigraphic zonation that, combined with radiometric ages from bentonite layers (Obradovich, 1993) and event-chronostratigraphic units (Kauffman, 1988), is almost peerless in its refinement. The most studied biostratigraphic schemes are for ammonites and bivalves (Obradovich and Cobban, 1975; Kauffman et al., 1993), and microplankton (Caldwell et al., 1993). A biostratigraphy of vertebrates in the Western Interior developed by Russell (1993) is much less detailed, recognising only four "ages" similar to the North American Land Mammal "Ages". The second to last, the Niobrara "Age," spans the Late Cenomanian to Early Campanian, and marks the appearance of mosasaurs in the Western Interior. The genera *Platecarpus*, *Ectenosaurus*, *Tylosaurus*, and *Clidastes* are typical of this "age," preserved in units such as the Niobrara Formation and the Pierre Shale (Sharon Springs and Pembina Members). In the final Navesinkian "Age," from the late Campanian to late Maastrichtian, a faunal turnover replaces the mosasaurs typical of the Niobrara "age" with *Mosasaurus*, *Prognathodon,* and *Plioplatecarpus*. This "age" is preserved in the Bearpaw Formation.

Introduction to Chapter 2: *Hainosaurus pembinensis* and the Pierre Shale

West of Morden, Manitoba, a low escarpment exposes the Pembina Member of the Pierre Shale. The Pierre Shale is an Early Campanian–Early Maastrichtian marine formation of fine-grained terrigenous clastics, with well-studied exposures that stretch from South Dakota to southern Manitoba. The Pembina Member itself is typically present as two distinct units: a lower, grey-black carbonaceous shale containing twenty to thirty thin, yellowish bentonite layers, and an upper yellow-brown shale. Gill and Cobban (1965) correlated the Pembina Member with the Sharon Springs Member of the Pierre Shale in the northern United States. Under the well-known ammonite biostratigraphy for the Western Interior, McNeil and Caldwell (1981) concluded that the lower, bentonite-rich unit corresponds to the Zone of *Baculites obtusus*. While Nicholls (1988) reported an age of Early Campanian, the *Baculites obtusus* Zone falls at the very base of the Middle Campanian (Gill and Cobban, 1966), around 80 Ma before present (Obradovich, 1993).

The lower unit of the Pembina Member preserves a diverse fauna of vertebrate and invertebrate fossils, including mosasaurs (Bardack, 1968; Martin and Stewart, 1981), exposed as a result of commercial bentonite mining. Beginning in 1972, staff and volunteers of the Morden and District Museum began collecting these fossils. Though they had the permission of the mine operators, fossil collecting was often accomplished quickly to minimise their disturbance, and on occasion was even performed at night under the illumination of car headlights! As a result, many fossils were collected hastily, and damaged or confused with other fossils, but over time the Morden Museum has accumulated the largest collection of fossil marine vertebrates in Canada. Elizabeth

Nicholls took on the daunting task of a more detailed catalogue of this large and varied collection for her Master's thesis (Nicholls, 1989), and her description of *Hainosaurus pembinensis* was only a small part of this project (Nicholls, 1988).

This species is represented by several specimens of varying completeness in the Morden and District Museum, as well as a type in the Miami Museum northwest of Morden. Nicholls was satisfied in diagnosing *Hainosaurus* on the basis of a larger number of "precaudal" vertebrae (those preceding the first chevron-bearing caudal), the greater length of the femur relative to the humerus, a smaller infrastapedial process of the quadrate, and relatively greater length of the external nares (Nicholls, 1988:1567). She diagnosed *H. pembinensis* by noting (1988:1566) that the teeth did not show evidence of the heterodonty observed by Dollo (1885:288), and by relatively longer supratemporal fenestrae. Lingham-Soliar (1992a) did not discuss either of Nicholls' (1988) diagnoses in the light of his new understanding of *H. bernardi*, but mentioned that *H. pembinensis* appears to lack most of his own diagnostic features. Lindgren and Siverson (2002) have noted that in its dental anatomy, *H. pembinensis* appears most similar to *Tylosaurus*.

At the midpoint of my thesis research I travelled to Morden to examine the material of *Hainosaurus pembinensis*, purely for comparative purposes. Many anatomical features of this species were incongruent with the *Hainosaurus* descriptions of Dollo (1885, 1887, 1889) and Lingham-Soliar (1992). During my examination of *H. pembinensis*, the anatomical inconsistencies in Nicholls' (1988) descriptions later suggested by Lindgren and Siverson (2002) were confirmed, and it was clear that an detailed report on the anatomy of this species was warranted. To this end, the principal focus of Chapter 2 is to provide an updated description of the anatomy of *H. pembinensis*.

Introduction to Chapter 3: P 2588.1 and the Bearpaw Formation of Saskatchewan

The Bearpaw Formation is a Late Campanian–middle Maastrichtian marine unit of fine-grained terrigenous clastics exposed from central Montana northward to southern Alberta and Saskatchewan. In the South Saskatchewan River valley, the Bearpaw is present as a series of alternating dark grey silty mudstones and brownish sandstones. Ammonite fossils are common in the area (Riccardi, 1983), and specimens of *Plioplatecarpus* and *Mosasaurus* have been collected (pers. obs.), along with an undescribed tylosaurine mosasaur that is the focus of Chapter 3. Caldwell (1968) recognised eleven members in the Bearpaw along the South Saskatchewan. Using foraminifera he correlated them with the *Didymoceras nebrascense* through *Baculites grandis* Zones of the Western Interior ammonite biostratigraphy (North and Caldwell, 1970; Caldwell et al., 1993), which range from the early Late Campanian to middle Maastrichtian.

This thesis began with the examination of an undescribed tylosaurine mosasaur collected from the Bearpaw on the shore of Lake Diefenbaker, in the South Saskatchewan River valley. This specimen, accessioned as P 2588.1 in the collections of the Royal Saskatchewan Museum, includes a well-preserved cranium, a vertebral column complete to the proximal caudals, and a mostly complete but dissociated appendicular skeleton. It was collected in the Snakebite Member of Caldwell (1968), which spans from the *Baculites cuneatus* through *Baculites jenseni* Zones, latest Late Campanian in age (Kauffman et al., 1993). Being younger than the known species of *Tylosaurus*, P 2588.1

was provisionally assigned to *Hainosaurus* after collection. In Chapter 3, the anatomy of this specimen is described in detail and compared to that of other tylosaurines.

Introduction to Chapter 4: Phylogeny and Taxonomy of Mosasaurs

The phylogenetic and taxonomic position of mosasaurs has been a subject of heated discussion ever since the discovery of *Mosasaurus hoffmani*. Cuvier (1808) concluded that this new creature should be allied with the iguanas and monitor lizards (*Varanus*). Goldfuss (1845) agreed that the skull shared many features with modern lizards, and the monitor lizard in particular. Never one to follow the opinions of others, Cope (1869) grouped mosasaurs in a new order named Pythonomorpha, and placed them on the same rank as Lacertilia (lizards), and Ophidia (snakes), as orders of Squamata. This taxonomy was later followed by Leidy (1873), Boulenger (1891), and Dollo (1894), with the important difference that Cope and Boulenger proposed a phylogenetic affinity between mosasaurs and the Ophidia, while Leidy and Dollo allied them with the Lacertilia. The characters Cope cited to show similarity between snakes and his Pythonomorpha were all systematically invalidated by Owen (1877), Marsh (1880), Baur (1890), and finally Williston (1898), and these authors proposed instead that mosasaurs should be placed within the Lacertilia.

The discovery of dolichosaurs (Owen, 1850) and aigialosaurs (Kramberger, 1892; Kornhuber, 1893, 1901) had an immediate effect upon the phylogenetic position of mosasaurs. A few authors, notably Osborn (1899), concluded that mosasaurs were too derived to have evolved from these groups, and were content to place the ancestor of mosasaurs amongst the Lacertilia of the early Mesozoic, allying dolichosaurs and aigialosaurs with the monitor lizards. A more popular view was that they were somehow ancestral to lizards, snakes, or mosasaurs, though there was debate over how this was accomplished. Boulenger (1891) considered dolichosaurs to be the source of lizards, snakes, and mosasaurs, while Kramberger (1892) proposed aigialosaurs as the ancestors of lizards and mosasaurs. Kornhuber (1901), Nopsca (1903), and Dollo (1904) considered aigialosaurs to be ancestral to the mosasaurs, but classified them both within the Lacertilia. Nopsca's (1908) suggestion that snakes evolved from dolichosaurs was strictly opposed by Camp (1923) and did not revive Cope's Pythonomorpha.

Another school of thought held that mosasaurs evolved from within the lizards. Baur (1890) believed that mosasaurs were true lizards and classified them with the monitor lizards in Superfamily Varanoidea. Williston (1904) agreed with his conclusions, but took the more conservative approach of grouping varanids, aigialosaurs, and dolichosaurs into Superfamily Platynota, and mosasaurs in Superfamily Mosasauria. Camp (1923) derived aigialosaurs from varanid lizards, and considered aigialosaurs ancestral to both mosasaurs and dolichosaurs. This systematic and phylogenetic position was maintained by Russell (1967), and has been supported by a variety of cladistic studies on the phylogeny of squamates (Rieppel, 1980; Carroll and deBraga, 1992; deBraga and Carroll, 1993). Other phylogenetic analyses, however, have placed the group containing aigialosaurs and mosasaurs (the Mosasauroidea) outside the Varanoidea (Gauthier, 1982; Pregill et al., 1986; Caldwell, et al. 1995; Caldwell, 1999).

Recent cladistic studies have returned support to Nopsca's (1908) phylogeny of dolichosaurs, placing them as the sister group to snakes (Lee and Caldwell, 2000; Pierce and Caldwell, 2004), though this position has not been endorsed by all authors (Rieppel and Zaher, 2000). Under this scheme the Dolichosauridae become paraphyletic, forming a series of sister groups to the Ophidia (Pierce and Caldwell, 2004). While Carroll and deBraga (1992) and deBraga and Carroll (1993) have assumed the monophyly of aigialosaurs, and their sister group position with the Mosasauridae, cladistic tests of this relationship indicate that the Aigialosauridae are also paraphyletic, forming progressive sister groups to the mosasaurids (Bell, 1993, 1997; Caldwell et al., 1995; Caldwell 1996).

In contrast to the inconstant position of mosasaurs within Squamata, the systematic and phylogenetic relationships within Mosasauria have remained remarkably constant over the last century. The earliest attempts at a classification of mosasaurs were plagued by incorrect anatomical descriptions. Cope (1869-1870) recognised two types of mosasaurs, naming them families Mosasauridae and Clidastidae, but his definition of the former was based upon the incorrect observation of fused pterygoids in *Mosasaurus missouriensis* (Goldfuss, 1845). Dollo (1884) also acknowledged two families of mosasaurs, including Cope's Mosasauridae and his own Plioplatecarpidae, but the latter was incorrectly diagnosed by a true sacrum, which he later realised was a pair of pathologically fused pygal vertebrae (Dollo, 1894). By 1890, Dollo recognised three types of mosasaurs, based on the size of the premaxillary rostrum: a microrhynchous type including *Platecarpus*, a mesorhynchous type including *Mosasaurus* and *Clidastes*, and a megarhynchous type including *Tylosaurus* and *Hainosaurus*.

The modern taxonomic scheme appeared when Williston (1897) formally named and characterised Dollo's microrhynchous, mesorhynchous, and megarhynchous types as the subfamilies Platecarpinae, Mosasaurinae, and Tylosaurinae, respectively. He recognised a fundamental division of mosasaurs into two types: Subfamily Mosasaurinae was united by complete ossification of the appendicular skeleton and fused haemal arches, while subfamilies Platecarpinae and Tylosaurinae shared incomplete ossification of the appendicular skeleton and articulated haemal arches. Russell (1967) employed Williston's subfamilies, but followed Dollo in using Plioplatecarpinae in place of Platecarpinae.

Russell's (1967:fig. 99) tree of mosasaur evolution (Fig. 1-7) reiterated Williston's (1898) separation of mosasaurs into those evolving from a *Clidastes*-like ancestor, the Mosasaurines, and those evolving from a *Platecarpus*-like ancestor, the Plioplatecarpines and Tylosaurines. The *Clidastes*-like ancestor gave rise to a stem of *Clidastes* species, from which *Mosasaurus* and *Globidens* branched early, followed by *Plotosaurus* and *Taniwhasaurus* as the descendants of derived *Clidastes*. The Plioplatecarpines and Tylosaurines diverged early from the *Platecarpus*-like ancestor. The Plioplatecarpine stem gave rise to the species of *Platecarpus*, before which evolved *Ectenosaurus* and *Halisaurus*. *Plioplatecarpus* and *Prognathodon* branched from within the lineage of *Platecarpus* species. The Tylosaurines formed a simple lineage from *T. nepaeolicus* to *T. proriger* to *Hainosaurus*.

A pair of related studies by Bell (1993, 1997) were the first cladistic attempts at a phylogeny of the Mosasauroidea. His preferred tree (Fig. 1-8) shares the general structure of Russell's phylogeny, but there are some key differences. The aigialosaurs are not a monophyletic grouping: "*Opetiosaurus*" (=*Aigialosaurus*) *buccichi* is the sister group to all other mosasauroids. Rather than being an offshoot of *Clidastes*, the species of *Plotosaurus* are nested within *Mosasaurus*, making *Mosasaurus* paraphyletic. *Halisaurus* moves dramatically from being the sister group to the plioplatecarpines to a position at the base of the mosasauroid radiation. *Plesiotylosaurus* nests within a paraphyletic *Prognathodon*, and together with the species of *Globidens* they form a clade inside the Mosasaurinae. Bell's (1997) 'Russellosaurines,' an informal grouping containing the plioplatecarpines and tylosaurines that is now designated parafamily Russellosaurina (Polcyn and Bell, 2005), have the same relationship as they do in Russell's phylogeny: *Platecarpus* remains paraphyletic, with the species of *Plioplatecarpus* nested at the crown of the Plioplatecarpini. The gross structure of Bell's (1993, 1997) phylogeny has been confirmed by Caldwell (1996) using a reduced data set supplemented by information from the anatomy of the mesopodium.

The final research chapter of this thesis, Chapter 4, is a phylogenetic analysis of the Mosasauroidea, with special emphasis on the Tylosaurinae.

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FIGURE 1-1. Cranial anatomy of mosasaurs: skull of *Platecarpus ictericus* (after Russell, 1967). **A**, lateral view. **B**, dorsal view. **C**, posterior view; and **D**, ventral view. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **en**, external naris; **f**, frontal; **in**, internal naris; **j**, jugal; **l**, lacrymal; **mx**, maxilla; **o**, orbit; **op**, opisthotic; **p**, parietal; **pmx**, premaxilla; **pof**, postorbitofrontal; **prf**, prefrontal; **pl**, palatine; **pr**, prootic; **pt**, pterygoid; **q**, quadrate; **sq**, squamosal; **st**, supratemporal; **stf**, supratemporal fenestra; **v**, vomer. Scale bar equals 50 mm.

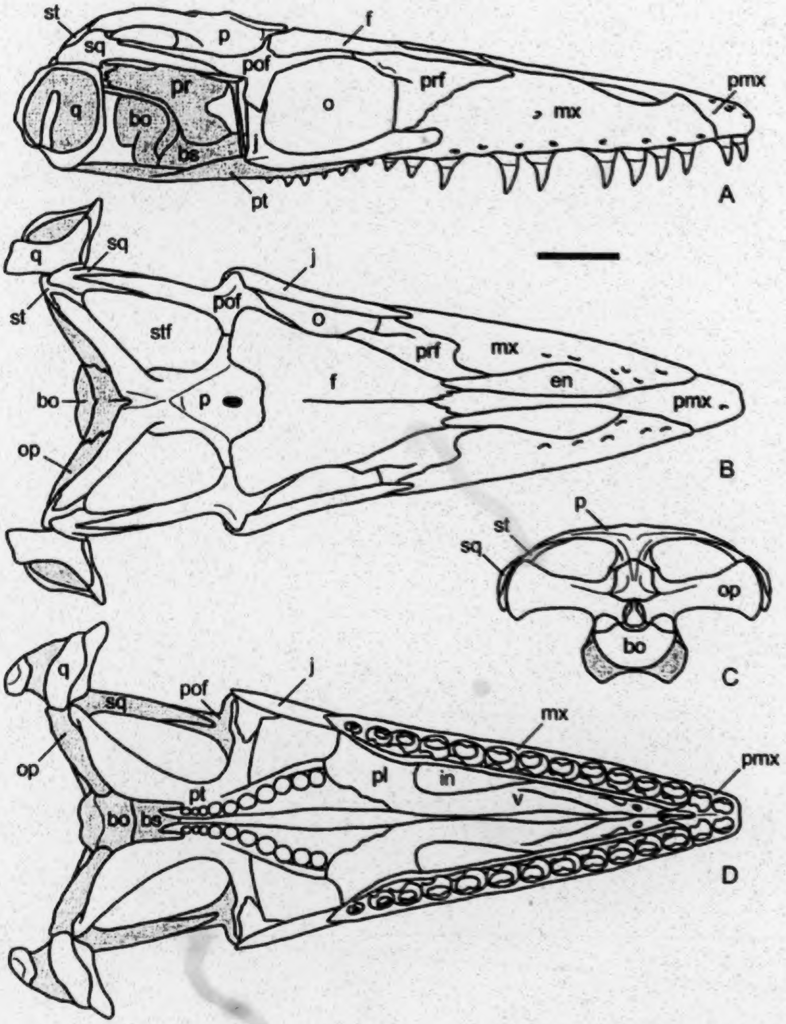
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FIGURE 1-2. Cranial anatomy of mosasaurs: mandible of *Platecarpus ictericus* (after Russell, 1967). **A**, lateral view; and **B**, medial view. **Abbreviations**: **a**, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **gf**, glenoid fossa; **par**, prearticular; **sa**, surangular; **sp**, splenial. Scale bar equals 50 mm.

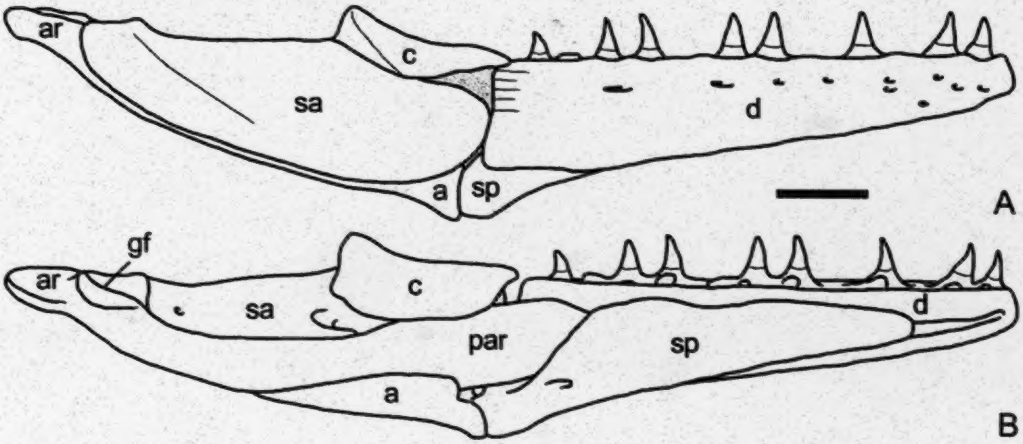
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FIGURE 1-3. Anatomical comparison of mosasaur quadrates. **A**, *Platecarpus ictericus* in lateral view showing external features (after Russell, 1967:fig. 25). **B**, *Platecarpus ictericus* in medial view showing internal features (after Russell, 1967:fig. 25). In lateral view: **C**, *Tylosaurus nepaeolicus* (after Russell, 1967:fig. 94); **D**, *Tylosaurus proriger* (after Russell, 1967:fig. 94); **E**, *Hainosaurus bernardi* (after Lingham-Soliar, 1992:fig. 9); **F**, *Mosasaurus maximus* (after Russell, 1967:fig. 80); **G**, *Clidastes propython* (after Williston, 1898:pl. 28); **H**, *Prognathodon rapax* (after Russell, 1967:fig. 91). **Abbreviations: isp**, infrastapedial process; **mn**, meatal notch; **mr**, median ridge; **patr**, posteroventral ascending tympanic rim; **sp**, stapedial pit; **ssp**, suprastapedial process; **ta**, tympanic ala; **tr**, tympanic rim. Not to scale.

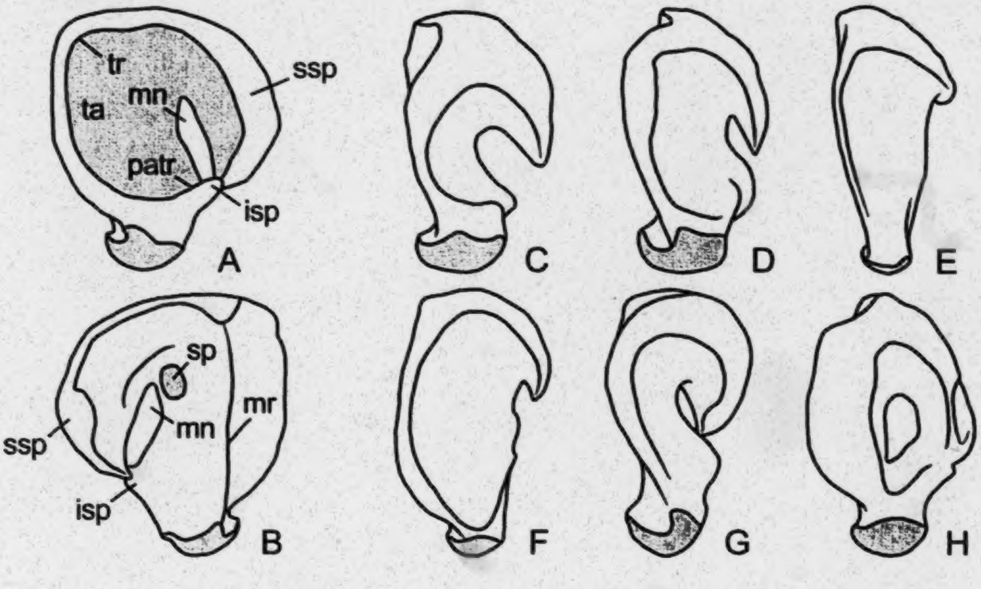

FIGURE 1-4. Appendicular skeletal anatomy of *Platecarpus ictericus* (after Russell, 1967). **A**, forelimb in ventral view; and **B**, hindlimb in ventral view. **Abbreviations**: **I–V**, metacarpals/metatarsals; **as**, astragalus; **ca**, calcaneum; **dc3**, third distal carpal; **dc4**, fourth distal carpal; **dt4**, fourth distal tarsal; **fe**, femur; **fi**, fibula; **hu**, humerus, **in**, intermedium; **ph**, phalanges; **ra**, radius; **ti**, tibia; **ul**, ulna; **ula**, ulnare. Scale bar equals 100 mm.

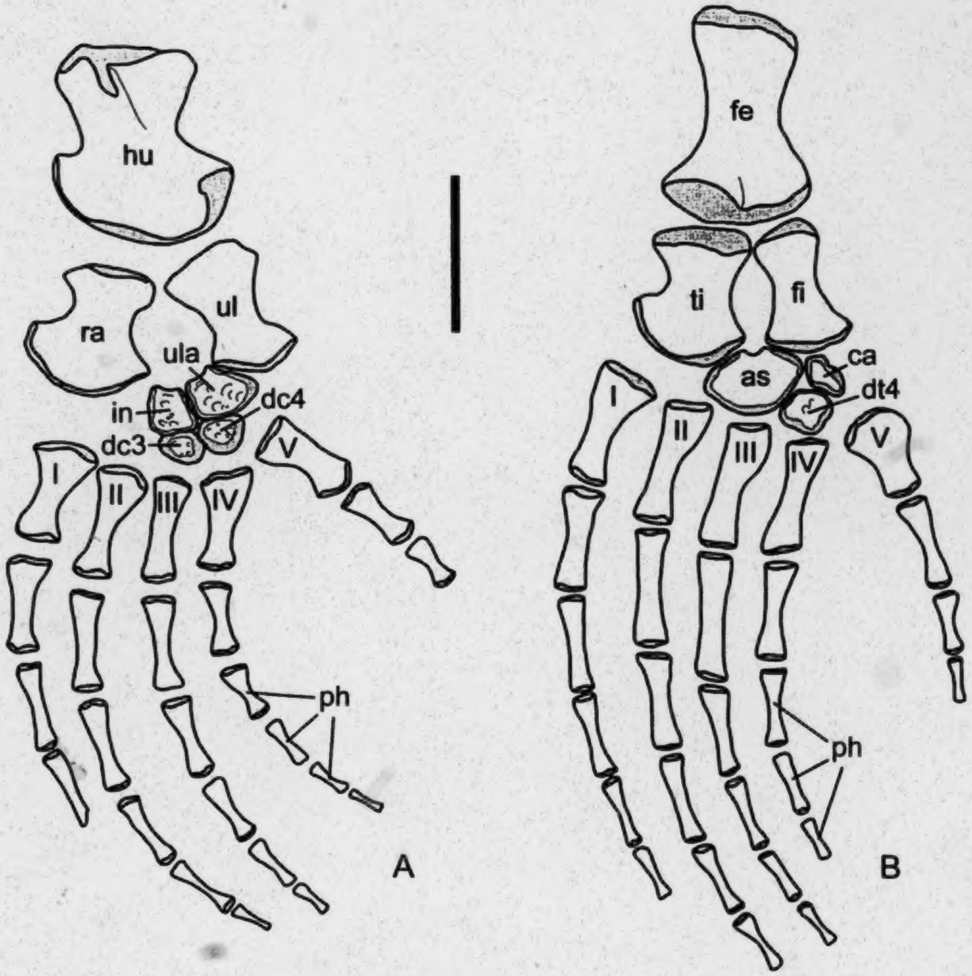
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FIGURE 1-5. Cranial anatomy of *Tylosaurus nepaeolicus* (after Russell, 1967). For abbreviations see Figs. 1-1–1-2. Scale bar equals 100 mm.

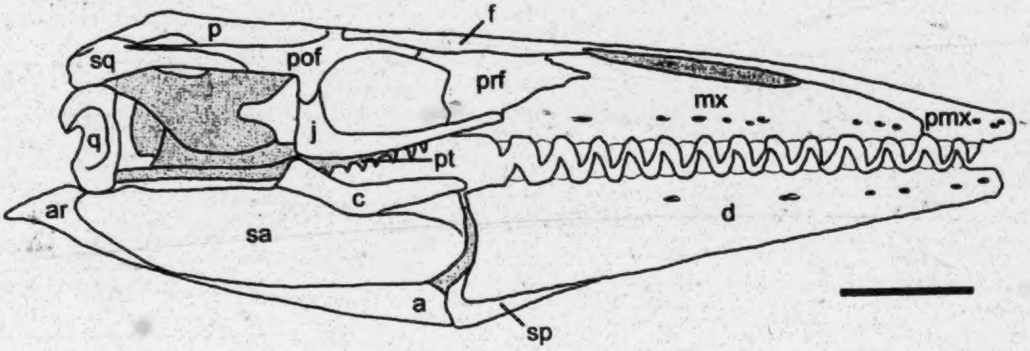
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FIGURE 1-6. Cranial anatomy of *Hainosaurus bernardi* (after Lingham-Soliar, 1992a). For abbreviations see Figs. 1-1–1-2. Scale bar equals 100 mm.

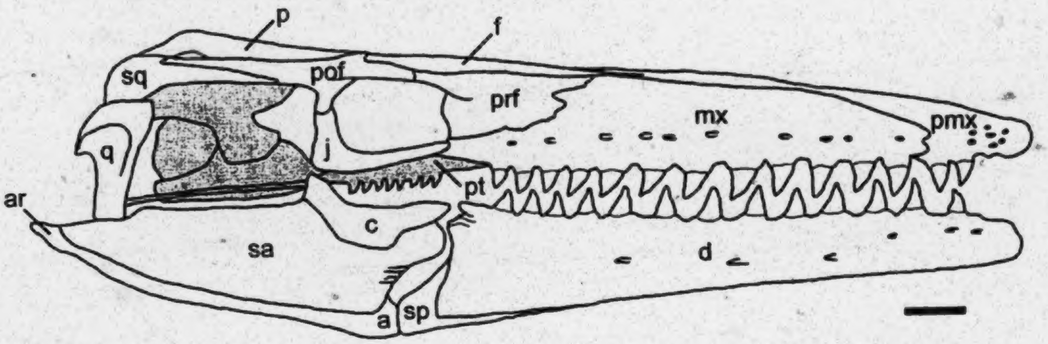
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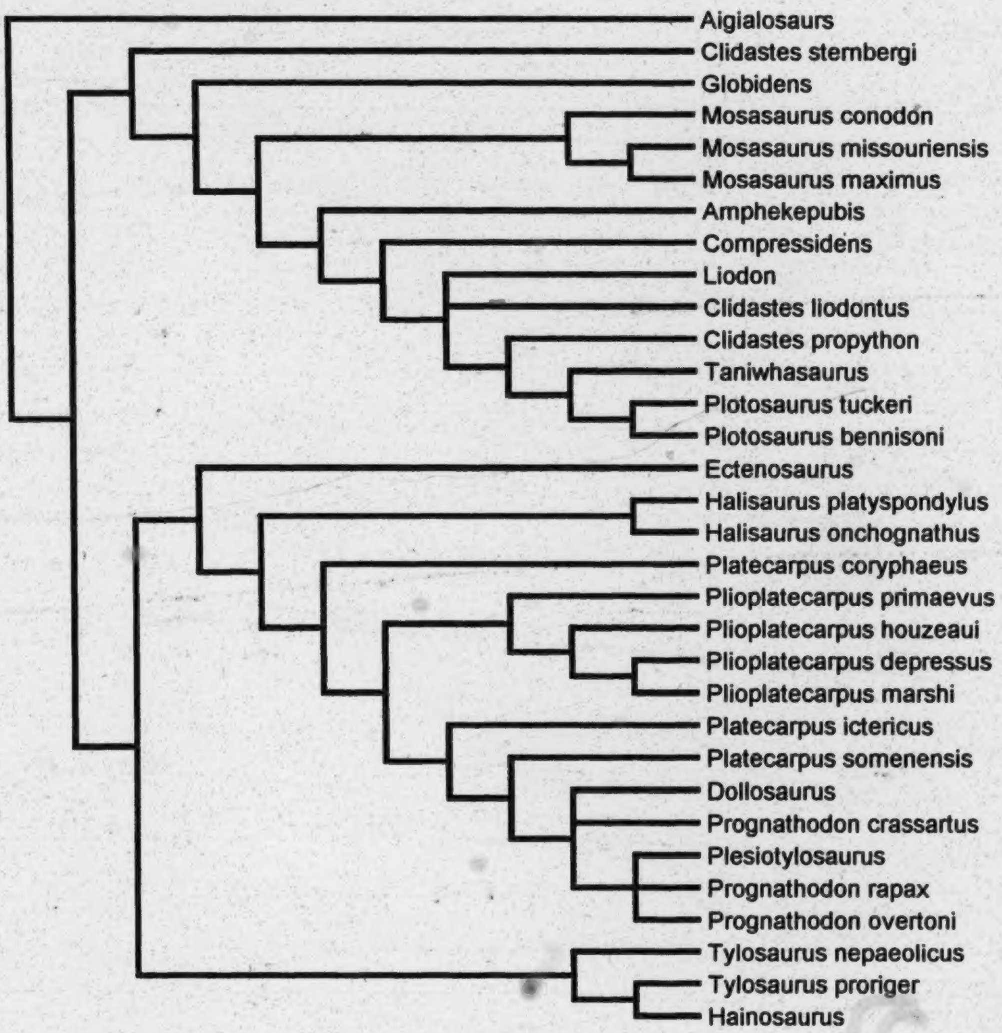
FIGURE 1-7. Russell's (1967:fig. 99) phylogeny of mosasaurs converted as accurately as possible into a cladogram.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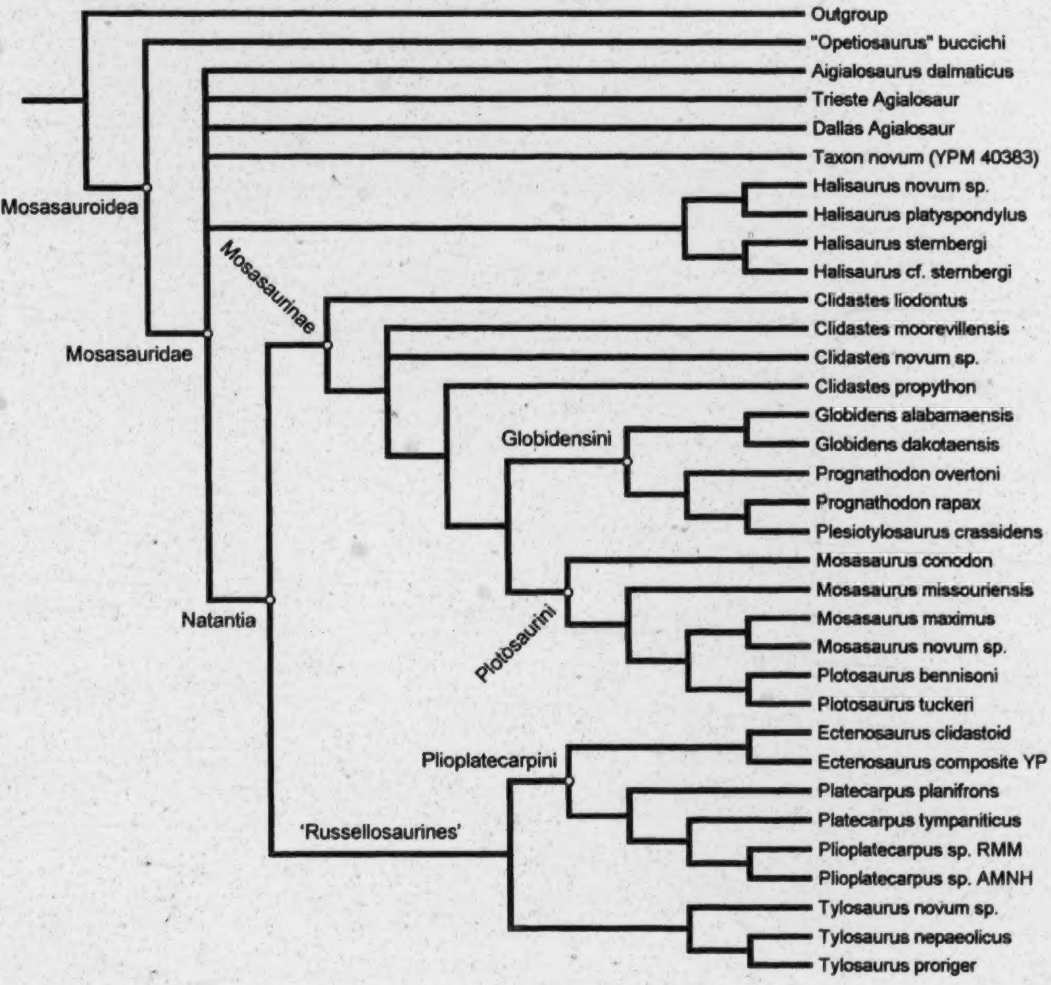
Clidastes sternbergi
Globidens
Mosasaurus conodon
Mosasaurus missouriensis
Mosasaurus maximus
Amphekepubis
Compressidens
Liodon
Clidastes liodontus
Clidastes propython
Taniwhasaurus
Plotosaurus tuckeri
Plotosaurus bennisoni
Ectenosaurus
Halisaurus platyspondylus
Halisaurus onchognathus
Platecarpus coryphaeus
Plioplatecarpus primaevus
Plioplatecarpus houzeaui
Plioplatecarpus depressus
Plioplatecarpus marshi
Platecarpus ictericus
Platecarpus somenensis
Dollosaurus
Prognathodon crassartus
Plesiotylosaurus
Prognathodon rapax
Prognathodon overtoni
Tylosaurus nepaeolicus
Tylosaurus proriger
Hainosaurus

FIGURE 1-8. Bell's (1997) preferred phylogeny of the Mosasauroidea, a strict consensus tree of 99 equally parsimonious trees of length 351 steps.


Outgroup
"Opetiosaurus" buccichi
Aigialosaurus dalmaticus
Trieste Agialosaur
Dallas Agialosaur
Taxon novum (YPM 40383)
Halisaurus novum sp.
Halisaurus platyspondylus
Halisaurus sternbergi
Halisaurus cf. sternbergi
Clidastes liodontus
Clidastes moorevillensis
Clidastes novum sp.
Clidastes propython
Globidens alabamaensis
Globidens dakotaensis
Prognathodon overtoni
Prognathodon rapax
Plesiotylosaurus crassidens
Mosasaurus conodon
Mosasaurus missouriensis
Mosasaurus maximus
Mosasaurus novum sp.
Plotosaurus bennisoni
Plotosaurus tuckeri
Ectenosaurus clidastoid
Ectenosaurus composite YP
Platecarpus planifrons
Platecarpus tympaniticus
Plioplatecarpus sp. RMM
Plioplatecarpus sp. AMNH
Tylosaurus novum sp.
Tylosaurus nepaeolicus
Tylosaurus proriger
Mosasauroidea
Mosasauridae
Mosasaurinae
Natantia
Globidensini
Plotosaurini
Plioplatecarpini
'Russellosaurines'

APPENDIX

What follows is an introduction to the osteological anatomy of mosasaurs, beginning with the cranial skeleton, the axial skeleton, and finishing with the appendicular skeleton. My intention is not to produce an exhaustive list of every element, nor to describe every feature of those elements, but to describe the anatomy that is relevant to the following chapters for the mosasaurs in which this anatomy is well established, as well as some of the functional anatomy that was important while mosasaurs were alive. Except were noted, all anatomical information is from Russell (1967). For more detailed descriptions, the reader is referred to the excellent anatomical reviews in Williston (1898), Camp (1942), and Russell (1967).

Cranial skeletal anatomy

The mosasaur cranium is a diagnostic structure and worthy of some detailed attention. In general shape, the skull is conical, tapering toward the snout in both dorsoventral and mediolateral aspects (Fig. 1-1). The mandibles converge anteriorly, and are deepest at their midpoint, at the very complex intramandibular joint (Fig. 1-2). About half of the length of the skull is the tooth-bearing snout, with a large orbit and a somewhat shorter temporal region behind.

The primitive diapsid condition of two fenestrations on either side of the skull behind the orbit is modified in squamates. The upper supratemporal fenestra, which is not to be confused with the supratemporal bone, is retained. The lower infratemporal fenestra, however, is no longer bound by the quadratojugal ventrally, thus creating an expansive open area on the cheek. The nostrils are long and thin, and placed dorsally on the elongate snout (Fig. 1-1B).

The premaxilla forms the tip of the snout and extends between the paired narial openings as far back as the frontal (Fig. 1-1B). While this is ancestrally a paired bone, it is always fused in mosasaurs, as it is in all squamates. There are four teeth, two on either side. The premaxilla ends directly above the first tooth in *Platecarpus* (Fig. 1-1A), *Plioplatecarpus*, *Prognathodon*, and *Plesiotylosaurus*, is extended into a short, conical rostrum in *Clidastes*, *Ectenosaurus*, and *Mosasaurus*, and is even further elongated into a rectangular 'prow' in *Hainosaurus* (Fig. 1-6) and *Tylosaurus* (Fig. 1-5).

The maxilla is a long element, bearing 20–24 teeth in *Halisaurus*, 18 teeth in *Plotosaurus*, 14–18 teeth in *Clidastes*, 14 teeth in *Mosasaurus* and *Prognathodon*, and 12–13 teeth in *Hainosaurus* (Fig. 1-6), *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus* (Fig. 1-5). In most mosasaurs it forms the lateral margin of the nares as far back as the prefrontal, but in *Ectenosaurus*, *Plotosaurus*, and *Tylosaurus* (Fig. 1-5) a posterior process of the maxilla overlaps the prefrontal to form the entire margin. The external nares begin where the maxilla and premaxilla diverge from each other, and end either in an emargination of the frontal or at the contact between the prefrontal and frontal. The nares vary in their contribution to the total length of the skull: 39% in *Plotosaurus*, 26–34% in *Prognathodon*, *Mosasaurus*, *Platecarpus*, and *Clidastes*, 28–31% in *Hainosaurus* (Lingham-Soliar, 1992a) and only 20–24% in *Tylosaurus* and *Plesiotylosaurus* (Russell, 1967). The lateral margin of the internal nares is also formed by the maxilla (Fig. 1-1C).

The maxilla extends backward as far as the anterior margin of the orbit, but its posterodorsal corner is notched to accommodate the prefrontal, a triangular bone that also contributes to the anterior orbital margin, as well as part of the dorsal margin (Fig. 1-1A). The upper edge of the prefrontal is overlain by the frontal except along the narial margin. A triangular ala is present on the supraorbital portion of the prefrontal in *Clidastes*, *Plesiotylosaurus*, *Plotosaurus*, *Prognathodon*, and *Mosasaurus*, this is reduced to a tuberosity in *Platecarpus* (Fig. 1-1A) and *Plioplatecarpus*. Between the maxilla and the prefrontal on the anterior orbital margin lies the lachrymal, a small triangular bone that is rarely preserved in mosasaur specimens (Fig. 1-1A).

The postorbitofrontal abuts against the prefrontal above the orbit in most mosasaurs, overlaps the prefrontal in *T. proriger*, and is well separated from the prefrontal in *Clidastes*. The postorbitofrontal is made of four divergent processes: an anterior process towards the prefrontal, a ventral one towards the jugal, a dorsal one towards the parietal, and a posterior one which overlaps the squamosal along the lateral margin of the supratemporal fenestra. The anterior process bears an ala similar to that on the prefrontal in *Clidastes*, and to a lesser extent in *Globidens*, *Mosasaurus*, *Plotosaurus*, and *Prognathodon*.

The jugal is "L-shaped," framing the posteroventral and ventral margins of the orbit (Fig. 1-1A). It continues ventrally from the postorbitofrontal's ventral process before turning forward to meet the maxilla near the lower edge of the orbit. The posteroventral corner of the jugal bears a small tuberosity in *Ectenosaurus*, *Platecarpus*, *Plotosaurus*, *Prognathodon*, *Mosasaurus*, *Tylosaurus*.

The frontal is a roughly triangular bone (Fig. 1-1B). Its anterior tip is narrow and forms the posterior portion of the internarial bar where it meets the premaxilla; in *Hainosaurus* (Fig. 1-6) and *Tylosaurus* (Fig. 1-5) the premaxilla forms the entire internarial bar and extends well onto the top of the frontal. From the nares, the margins diverge laterally and there is usually a gentle to strong emargination above the orbits. A raised keel along the midline of the frontal is variably present, even within the same species. At its posterolateral corner the frontal margin turns sharply medially, forming a roughly straight suture with the parietal in *Clidastes*, *Hainosaurus*, and *Tylosaurus* but a more sinuous one in other mosasaurs where tongues of the frontal overlap the opposing element.

The parietal is "Y-shaped:" an anterior portion divides the supratemporal fenestrae medially, then bifurcating into two suspensorial rami that form the posterior borders of the fenestrae (Fig. 1-1B). The parietal bears a large foramen on its anterior end which housed the pineal organ in life. This foramen is large and located deep within the frontal in *Plioplatecarpus*, partly within the frontal in *Hainosaurus* and *Platecarpus* (Fig. 1-1B), within the parietal but close to the frontal suture in *Clidastes*, *Globidens*, *Mosasaurus*, *Plotosaurus*, and *T. proriger*, and well behind the suture in *Ectenosaurus*, *Halisaurus*, and *T. nepaeolicus*. The anterior portion of the parietal is roughly rectangular in outline, though the anterolateral margins may continue as a pair of crests onto the dorsal surface, converging towards the rear of the element. The ventral surface bears a pair of lateral wings that extend down to meet the braincase and form the medial wall of the supratemporal fenestrae. These wings are roughly semicircular in lateral outline; in *Plotosaurus* they are particularly large and fuse with the bones of the braincase. The parietal's suspensorial rami are vertically compressed and extend laterally to meet the main body of the supratemporal next to the quadrate. The ventral surface of each ramus is covered by a thin extension of the supratemporal; in *Plotosaurus*, *Prognathodon*, and *Tylosaurus* the parietal also 'sandwiches' the supratemporal ventrally with another thin process.

Along the palate are a series of bones: a pair of long thin palatines that extend between the maxillae and define the medial border of the internal naris, and behind them the paired pterygoids (Fig. 1-1C). The pterygoid is composed of a main tooth-bearing axis, a posterolateral process that meets the quadrate, and an anterolateral process towards the jugal. The main axis is sutured to the palatines anteriorly, at its posterior end it forms a wing that meets the basisphenoid. On its ventral surface the main axis bears a row of teeth on a raised rim; this row is usually slightly sinuous in outline when viewed ventrally (Fig. 1-1C). There are 14–16 pterygoid teeth in *Clidastes*, 12–15 teeth in *Plotosaurus*, 10–12 teeth in *Platecarpus* (Fig. 1-1C), 10–11 teeth in *Hainosaurus* and *Tylosaurus*, 7–10 teeth in *Mosasaurus*, and 7 teeth in *Prognathodon*.

The mosasaur braincase is composed of several solidly-sutured bones. At its posteroventral end, the basioccipital forms the hemispherical occipital condyle (Fig. 1-1D). The dorsal surface of the basioccipital is excavated to form the posterior half of the medullary cavity, the remainder is formed by the basisphenoid anteriorly. Resting on top of the basioccipital and forming the posterior roof of the medullary cavity are the fused opisthotic and exoccipital. The exoccipitals form a small portion of the occipital condylar surface laterally, while the opisthotic sends a robust para-occipital process posterolaterally to brace the supratemporal from within. Resting on top of the basisphenoid and forming the anterior roof of the medullary cavity is the prootic. The otosphenoid crest of the prootic is uniquely expanded in *Tylosaurus*, covering most of the ventral opisthotic. The internal auditory meatus originates in a groove between the prootic and the opisthotic, and the inner ear itself is housed in a cavity within the prootic. The prootic sends an elongate process posterolaterally that overlies the paraoccipital process of the opisthotic and is sutured to the supratemporal (Fig. 1-1A).

The supratemporal is a thin element that lies along the dorsolateral portion of the paraoccipital process of the opisthotic (Fig. 1-1D). Its lateral tip is held between the expanded head of the squamosal and the distal end of the paraoccipital process; a small area of the bone is exposed here and it forms part of the articular surface for the quadrate. The squamosal is a long bone with an expanded head that underlies the posterior process of the postorbitofrontal. Its head is sutured to the supratemporal medially and sends a short process to meet the suspensorial ramus of the parietal dorsomedially. The ventral margin of the head forms a curved articular facet which receives the dorsal head of the quadrate.

The quadrate forms the link between the skull, via the suspensorium, and the mandible, and is an extremely important diagnostic element in mosasaurs (Fig. 1-3). In general form the quadrate is a nearly vertical shaft with dorsal and ventral articular condyles. From the posterior face of this shaft are developed a pair of processes. The dorsal suprastapedial process is the larger of the two, curving posteroventrally and often slightly medially to enclose the meatal notch. The ventral infrastapedial process is often triangular in outline and does not extend far from the shaft. A thin, concave tympanic ala is developed from the anterolateral edge of the quadrate shaft. The curved edge of this ala, the tympanic rim, begins on the lateral face of the suprastapedial process, curving anterolaterally before turning in a downward arc nearly to the ventral condyle, and then curving upward again to join the infrastapedial process in *Ectenosaurus*, *Platecarpus*, *Plioplatecarpus*, and *Prognathodon*. In *Clidastes* and *Tylosaurus* the infrastapedial is separate from the tympanic ala, but the tympanic rim is present as a crest that terminates on the lateral face of the process. The infrastapedial is reduced to a mere tuberosity on the centre of the posterior shaft in *Hainosaurus*, *Mosasaurus* and *Plotosaurus*. The suprastapedial is long, nearly meeting the infrastapedial process in *Platecarpus* and *Plioplatecarpus*, of moderate length in *Clidastes* and *Tylosaurus*, short in *Hainosaurus* and *Mosasaurus*, and fused to the infrastapedial process in *Ectenosaurus*, *Prognathodon*, and *Plesiotylosaurus*. On the medial face of the shaft, near the top of the meatal notch, there is a depression, the stapedial pit, which is oval in *Clidastes*, *Mosasaurus*, *Platecarpus*, and *Plotosaurus*, kidney-shaped in *Plioplatecarpus*, circular in *Prognathodon*, and rectangular in *Hainosaurus* and *Tylosaurus*. The stapedial pit marks the point of articulation of a rounded process of the extracolumella, a slender rod of bone that passes through the meatal notch and transmits auditory vibrations from the tympanum (eardrum) to the stapes.

The dentary is a long, deep bone that forms most of the anterior half of the mandible (Fig. 1-2A). It bears 20–24 teeth in *Halisaurus*, 16–18 teeth in *Clidastes*, 14–17 teeth in *Mosasaurus*, 17 teeth in *Plotosaurus*, 14 teeth in *Prognathodon*, 13 teeth in *Ectenosaurus*, *Hainosaurus* (Fig. 1-6), and *Tylosaurus* (Fig. 1-5), and 12 teeth in *Platecarpus* and *Plioplatecarpus*. The tip of the dentary is extended beyond the anteriormost tooth in *Hainosaurus* and *Tylosaurus*, forming a rectangular prow similar to that on the premaxilla, only slightly extended in *Clidastes*, *Mosasaurus*, and *Plotosaurus*, and finishes directly in front of the first tooth in *Platecarpus* (Fig. 1-2A), *Plioplatecarpus* and *Prognathodon*. The medial face of the dentary is excavated by a deep channel; lying along the ventral edge of the channel is the splenial (Fig. 1-2B). This is a slender bone that is poorly exposed in lateral view, but bears a tall, thin wing of bone that extends dorsally to cover much of the medial dentary. At its posterior tip the splenial bears a circular to elliptical surface for articulation with the angular; this is the intramandibular joint.

The angular lies along the ventral margin of the posterior mandible, bearing on its anterior tip a triangular articular surface that matches a corresponding surface on the splenial. The angular is overlapped laterally by the surangular, a broad sheet of bone that forms most of the lateral face of the posterior mandible (Fig. 1-2A). In outline the surangular is roughly triangular, tapering to its posterior tip at the glenoid fossa. The anterodorsal corner of the surangular forms a rounded shoulder, on which rests the saddle-shaped coronoid. The surangular contributes half of the glenoid fossa, a hemispherical surface that faces dorsomedially. The other half is formed by the articular, a long, thin bone that is little exposed laterally. Behind the glenoid fossa, the articular bears a retroarticular process that is variable in lateral outline: triangular in *Clidastes*, rectangular in *Mosasaurus* and *Plotosaurus*, circular in *Globidens* and *Platecarpus*, and convex above but straight below in *Hainosaurus* (Fig. 1-6) and *Tylosaurus* (Fig. 1-5). The articular is fused with the prearticular, a long vertical sheet of bone that extends anteriorly past the intramandibular joint to finish in the channel between the dentary and splenial (Fig. 1-2B).

The early practice of naming taxa for isolated tooth crowns has created many complications for mosasaur taxonomy. Several modern species, such as *Tylosaurus ivoensis* and *Liodon anceps*, are based on types that are little more than tooth material. The tooth crowns of mosasaurs are composed of a thin layer of enamel sheathing a thicker, hollow layer of dentine; the crown is attached to a bony tooth base which is cemented into the alveolus. In general, marginal tooth crowns are conical in form, slightly recurved, and bear a raised carina on the anterior and posterior faces that can be faintly serrated. These carinae divide the crown into an inner lingual surface and an outer buccal surface, and are often displaced buccally to make the lingual surface convex and expanded relative to the flat buccal surface. In many mosasaurs the buccal surface is rotated anteriorly on teeth at the front of the jaw. Tooth morphology is generally similar in the same position on upper and lower jaws. Pterygoid teeth are usually much smaller than the marginal teeth, and more strongly recurved. In *Prognathodon* and *Plesiotylosaurus*, however, the anterior pterygoid teeth are equal in size to the marginal teeth, and decrease in height towards the posterior of the element.

The teeth of *Mosasaurus* are large and asymmetrical, with strong, serrated carinae. The buccal enamel surface is divided by vertical ridges into two or three distinct facets. Teeth of *Clidastes* are laterally compressed and asymmetrical, with well-developed, unserrated carinae. The enamel surface is usually smooth, but many immature specimens and some older individuals have three distinct buccal facets (Bell, 1997). Teeth in *Platecarpus* and *Plioplatecarpus* are slender and nearly circular in cross section; carinae are present but become weaker as the crown develops. Both crown surfaces are strongly facetted and ornamented with fine vertical striations. In

Hainosaurus and *Tylosaurus* the enamel is weakly facetted, with fine vertical striations at the base of the crown, and the carinae are serrated. The carinae of *Tylosaurus* are weak, however, while those of *Hainosaurus* are quite pronounced. Crowns of *Tylosaurus* are round in cross section, with an enlarged lingual surface, while those of *Hainosaurus* have a laterally compressed section and the surfaces are nearly equal (Lindgren and Siverson, 2002). The teeth of *Globidens* are squat and inflated so that they are nearly circular in lateral profile, with an enamel surface roughened by coarse ridges.

Non-skeletal skull organ systems

The orbits of mosasaurs are large compared to skull size, and the preservation of sclerotic plates in *Clidastes*, *Platecarpus*, *Plioplatecarpus*, *Prognathodon*, *Mosasaurus*, and *Tylosaurus* shows that the eye was also large and nearly filled the orbit. Mosasaur vision would have been directed laterally and slightly dorsoanteriorly in life (Russell, 1967). Olfaction in mosasaurs can be crudely inferred from the impressions of the olfactory lobes on the ventral surface of the frontal, and these are relatively smaller than in living lizards. A foramen in the anterior vomer is thought to be the opening for the Jacobson's organ, and this has given rise to the speculation that mosasaurs may have had forked tongues for 'tasting' the water. Well-preserved quadrates from several mosasaur specimens show that the cavity created by the tympanic ala was covered by a thin sheet of bone, presumed to be a calcified tympanum, which may have been fused to the extracolumella. The diameter of this calcification is slightly smaller than that of the surrounding tympanic rim, suggesting that it was suspended in the quadrate by the tympanic membrane. Russell (1967) theorised that the calcified tympanum functioned like a fish otolith to facilitate hearing in an aquatic medium.

Cranial kinesis

When considered as an entire functional unit, the mosasaur cranium is a dynamic structure that in some ways resembles the loose, flexible skull of snakes (Lee et al., 1999). Cranial kinesis in mosasaurs has been described in detail by Russell (1964) and Callison (1967). The bones of the muzzle, from the premaxilla back to the frontal, comprise a solid unit that articulates along a transverse mesokinetic axis with the parietal, allowing vertical movement of the anterior skull. Motion on this axis was restricted by overlapping flanges of the parietal and frontal; in *Mosasaurus*, *Plesiotylosaurus*, *Plotosaurus*, *Prognathodon*, and *Ectenosaurus* the frontal overlaps well onto the parietal and significantly reduces mesokinetic mobility. A second major articulation, the longitudinal metakinetic axis, between the descending processes of the parietal and the upper surface of the solid braincase unit, allowed the braincase to rotate independently about the occiput. On the palate, the pterygoid was anchored posteriorly by ligaments to the adjacent quadrate, as well as by muscles to the braincase and mandible, and anteriorly by an overlapping suture with the palatine, and would not have had much mobility. The quadrate rotated within the sagittal plane, protracting and retracting the mandible, but was also restricted in its movement by mandibular musculature and its involvement with the auditory apparatus.

The mosasaur mandible can be thought of as two separate units dividing the jaw roughly in half: an anterior unit consisting of the splenial and dentary, and a posterior unit consisting of the angular, surangular, coronoid, and articular. These units articulated on the intramandibular joint between the splenial and angular. The prearticular extends across this joint and prevented free movement. In *Platecarpus* and *Plioplatecarpus*, horizontal ridges on the articulating face of the angular and corresponding grooves on the splenial show that the intramandibular joint is essentially ginglymoid, restricted to movement in the frontal plane (Bell, 1993). This is evidence against Russell's (1964) hypothesis that the intramandibular joint flexed vertically to absorb shocks when impacting prey. Instead, the motion was chiefly lateral, allowing the mandible to expand outwards and increase the size of the gape (Lee et al., 1999). The prearticular would have acted like a spring to return the jaw to its normal shape (Bell, 1993). The anterior tips of the dentaries were not fused but instead united by a ligamentous joint that could accommodate the increase in gape.

Vertebral skeletal anatomy

The mosasaur vertebral column may be divided into cervical, dorsal, and caudal divisions, but as we shall see the distinction between these regions can be very subtle. The first two cervical vertebrae are uniquely constructed and conservative in form. The first, the atlas, is composed of four separate ossifications: a median centrum that articulates between the occipital condyle of the skull and the next vertebra, a pair of lateral neural arches whose processes meet above the centrum to contain the spinal cord, and a ventral hypapophysis that lies between the occipital condyle and the centrum. The hypapophysis and neural arches are joined together to form a ring-like structure, while the centrum attaches to the second cervical. The neural arches bear short lateral processes, called synapophyses, which articulate with short cervical ribs.

The second cervical, the axis, more closely resembles a typical vertebra. The neural arches are solidly fused to the centrum, and bear at their posterior base a pair of zygopophyses, tongue-like processes that articulate with matching structures on the opposite vertebrae to increase stability of the vertebral column. In *Clidastes*, *Mosasaurus*, *Ectenosaurus*, and *Globidens* there are also zygosphenes and zygantra, smaller interlocking processes located between the zygopophyses. Solidly wedged between the atlas centrum and the axis is the axis hypapophysis. The axis centrum bears a circular articulation on its ventral surface; here the hypapophysis of the succeeding vertebra is articulated.

The remaining cervicals resemble the axis in form. The centrum varies from circular to oval in cross section between different species. Zygopophyses are present on all remaining cervicals, as are zygosphenes and zygantra for species that possess them. Synapophyses are increasingly developed laterally on the centra as the ribs become larger. Hypapophyses are short, conical, slightly recurved bones that are freely articulated with the preceding centrum. The number of cervicals bearing such hypapophyses varies, in some species the posterior cervical centra have only a protuberance in the place of a hypapophyseal articulation, but hypapophyses never occur outside the cervical series. The shape of posterior cervicals is very similar to that of the anterior dorsals, and the division between these regions can only be located by identifyng the first rib that meets the sternum. In the few mosasaur specimens where this is possible the total number of cervical vertebrae appears to vary between seven in *Platecarpus* and

Tylosaurus (Osborn, 1899; Williston, 1910) and ten in *Hainosaurus* (Dollo, 1887) and *Plotosaurus* (Camp, 1942).

Anterior dorsal vertebrae have circular or oval centra, but posteriorly in the series they become increasingly triangular, with one apex of the triangle pointing dorsally. The dorsal series can be subdivided into a thoracic series with long ribs, not all of which meet the sternum, and a lumbar series with shorter ribs. There is no justification for separating these two based on the shape of the synapophyses, which remain large and well developed on all dorsal centra. The number of zygopophyses present along the dorsal series varies between species, but these articulations never extend the full length of the region. Zygosphene-zygantrum articulations become obsolete early in the dorsals in *Mosasaurus*, but in *Clidastes* and *Ectenosaurus* they continue to the end of the series. The termination of the dorsal region has been debated because the pelvic girdle of mosasaurs never articulates directly with the vertebral column. A modern consensus, supported by many authors (Merriam, 1894; Williston, 1898; Osborn, 1899; Camp, 1942), is that the first caudal vertebra is marked by synapophyses that are twice as long as those of the preceding dorsal, and thus that this first caudal represents the 'sacrum.' Using this rule, the number of dorsal vertebrae varies considerably, between 22–23 in *Tylosaurus* (Osborn, 1899) and 44 in *Plotosaurus* (Camp, 1942).

The caudal series can be subdivided into three distinct regions: a pygal region with synapophyses but lacking haemal arches, an intermediate region with haemal arches and synapophyses, and a terminal region with haemal arches but lacking synapophyses. Pygals have a triangular centrum like posterior dorsals, but backwards in the tail the centra become laterally compressed and taller than wide. Beginning with the intermediate caudals, each centrum bears a forked haemal arch ventrally. In *Ectenosaurus*, *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus* the haemal arch articulates with a pair of circular facets on the centrum, while in *Clidastes*, *Mosasaurus*, *Prognathodon*, *Globidens*, and *Plotosaurus* the haemal arches are immovably fused to the centrum. The neural spines of caudal vertebrae are typically tall, giving the tail the depth needed for propulsion; in some mosasaurs there is a region near the end of the tail where the spines are especially tall, giving the tail a lobe that may have aided in swimming. The total number of caudal vertebrae varies widely between species, from approximately 80 in *Clidastes* to 120 in *Tylosaurus*, and the distribution of vertebrae within the caudal regions is also variable.

Appendicular skeletal anatomy

The pectoral girdle contains at least two ossifications, the scapula and coracoid, and in some species the clavicle and interclavicle are also ossified. Certain exceptional specimens (Marsh, 1880; Osborn, 1899; Williston, 1910; Camp, 1942) show that there was also a cartilaginous sternum, as well as extensive suprascapular cartilages that would have significantly increased the area for muscle insertion on the scapula (Lingham-Soliar, 1992b, 1999). The coracoid is a fan-shaped bone that narrows to a neck where it meets the scapula. Towards the anterior margin, the neck is pierced by a foramen for the nerve of the M. supracoracoideus. A deep emargination from the medial edge of the coracoid that leads towards this foramen is variably present: it is totally absent in *Plotosaurus*, *Plesiotylosaurus*, *Prognathodon*, and *Mosasaurus*, present in young individuals of *Clidastes* but not in adults (Bell, 1993), present in some individuals of *Platecarpus*, seemingly without ontogenetic significance (Bell, 1993), and never present as more than a slight notch in *Ectenosaurus* and *Tylosaurus*. The scapula is also roughly fan-shaped, but expands more posterodorsally. In *Plotosaurus* and *Plioplatecarpus* the scapula is much larger than the coracoid. In *Clidastes*, *Mosasaurus*, and *Platecarpus* it is roughly the same size, while in *Hainosaurus* and *Tylosaurus* the scapula is much smaller. The scapula and coracoid each contribute half of the glenoid fossa, which faces obliquely laterally and posteriorly.

The proximal humerus forms a condyle that articulates with the glenoid (Fig. 1-4). Behind this condyle is a raised postglenoid process, that served as the point of insertion for muscles from the pectoral girdle. On the anterior edge of the glenoid condyle is a deltoid tuberosity; the pectoral crest is present on its ventral face. The shaft of the humerus is constricted at its midpoint but expands again distally. The distal end of the shaft is separated into two large articular facets: an anterior radial facet and a posterior ulnar facet. Above these facets are prominent entepicondylar and ectepicondylar tuberosities, respectively. The tips of these tuberosities are roughened for muscle attachment. In *Clidastes*, *Mosasaurus*, and *Plotosaurus*, the humerus is short, nearly as broad as it is long. The processes and tuberosities are all well developed. The same is not true for the humerus of *Hainosaurus*, *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus*, where the processes and tuberosities are merged almost indistinguishably into proximal and distal articular surfaces (Fig. 1-4A). These surfaces are unfinished, and would have been capped by thick cartilages in life. In *Platecarpus* and *Plioplatecarpus* the humerus is slightly elongated, but in *Hainosaurus* and *Tylosaurus* it is very long and slender. The humerus of *Platecarpus* and *Tylosaurus* has a deep groove or tunnel above the radial facet on the dorsal surface that may have been the passage for the radial nerve.

The radius and ulna are both roughly the same length as the humerus (Fig. 1-4A). Their proximal ends are expanded for articulation with the humeral facets. The distal end of the radius is expanded into a flange that curves out onto the anterior face of the bone. It has a distal facet for the radiale. The proximal ulna bears an olecranon process on the posterior edge. Its distal end forms three facets, a large medial facet for the ulnare and two smaller facets for the intermedium and pisiform. In *Hainosaurus* and *Tylosaurus*, these processes of the radius and ulna are weakly developed, giving the bones a slender outline. The posterior margin of the radius and the anterior margin of the ulna border an antebrachial foramen that is nearly circular in *Clidastes*, *Ectenosaurus*, *Platecarpus* (Fig. 1-4A), and *Plioplatecarpus*, oval in *Mosasaurus*, and an elongate oval in *Hainosaurus* and *Tylosaurus*.

The carpus contains 7 ossifications in *Clidastes*, *Mosasaurus*, and *Plotosaurus*: a radiale, intermedium, ulnare, and pisiform in the proximal row from anterior to posterior, and second, third, and fourth distal carpals in the distal row. The intermedium borders on the antebrachial foramen in most mosasaurs, but is excluded by the distal ends of the radius and ulna in *Plotosaurus*. The carpus of *Platecarpus* is less ossified, containing only the ulnare, intermedium, and third and fourth distal carpals, and both the intermedium and ulnare border the antebrachial foramen (Fig. 1-4A). In *Tylosaurus* and *Hainosaurus* the carpus is poorly ossified, containing only two rounded elements in the positions of the ulnare and fourth distal carpal. Metacarpals and phalanges are usually slender, cylindrical, and slightly expanded at both ends. The bones of the first digit are often broader than the other digits, especially in *Clidastes* and *Mosasaurus*. In many mosasaurs the fifth digit diverges slightly to the posterior. Phalangeal formulae vary from 4-5-5-5-3 in *Clidastes*, 9-10-10-10-4 in *Mosasaurus*, 4-6-7-5-3 in *Platecarpus*, to 5-7-9-10-11 in *Tylosaurus*.

The pelvic girdle of mosasaurs contains the usual three elements: a dorsal ilium, anterior pubis, and posterior ischium. The ilium has an expanded, ventral head, which narrows into an anteriorly-oriented shaft. The pubis is similar in shape, but its shaft is shorter and directed anteroventrally and medially. The anterior edge of the proximal shaft is developed into a process that is large and rectangular in *Clidastes*, triangular in *Mosasaurus* and *Platecarpus*, and reduced to a ridge in *Tylosaurus*. The obturator foramen pierces the pubis shaft towards its proximal head. The ischium has a broader shaft than the other bones. On the posterior margin is an ischiadic tubercle that is especially pronounced in *Tylosaurus*. Each of these bones bears three proximal facets, one for each of the adjoining bones, and a lateral facet that contributes about one-third of the acetabulum. In *Platecarpus* and *Tylosaurus* these articular facets are not distinct.

The femur is a more slender bone than the humerus (Fig. 1-4B). It is roughly the same length as the humerus in *Clidastes*, *Mosasaurus*, *Platecarpus*, and *Tylosaurus*, but distinctly shorter in *Prognathodon* and slightly longer in *Hainosaurus*. There is a small internal trochanter on the anteroventral corner of the proximal shaft. The distal end of the shaft bears two facets: a larger anterior facet for the tibia, and a smaller posterior facet for the fibula. A tuberosity is developed above the anterior edge of the tibial facet. The femora of *Mosasaurus* and *Clidastes* follow this basic pattern, but in *Mosasaurus* the bone is more robust. In *Platecarpus*, *Hainosaurus*, and *Tylosaurus* the distal end of the femur is considerably wider than the proximal, and the internal trochanter is slightly reduced in size (Fig. 1-4B). Like the humerus in these genera, the proximal and ventral articular surfaces are rough and unfinished, and would have been capped by thick cartilages in life.

The tibia and fibula are slightly shorter than the femur (Fig. 1-4B). Their proximal ends are expanded for articulations with the femoral facets. The tibia is broader than the fibula, but slightly constricted at its midpoint. The distal end bears a flange that curves onto the anterior margin of the bone, this is especially developed in *Tylosaurus*. The distal articular surface bears a facet for the astragalus. The fibula is slender and slightly expanded at both ends. A small posterior flange is present on the distal end of the shaft in *Tylosaurus*. The posterior margin of the tibia and the anterior margin of the fibula border a crural foramen that is oval in outline.

Only three elements are present in the tarsus of mosasaurs: the astragalus, calcaneum, and fourth distal carpal. The astragalus is large with facets for the tibia and fibula. There is a groove in the proximal margin marking the entrance of the perforating artery (Caldwell, 1996). In *Platecarpus* there is a small emargination bordering the crural foramen (Fig. 1-4B); this is very small or missing in *Tylosaurus*. The calcaneum is not ossified in *Tylosaurus*. Metatarsals resemble the metacarpals very closely, but the fifth metatarsal tends to be broader and more strongly flexed than the fifth metacarpal. The phalanges are slender and only slightly expanded, but tend to be broader in the first digit. As in the manus, the fifth pedal digit is often divergent to the posterior. Phalangeal formulae vary from 8-9-9-9-4 in *Mosasaurus*, 4-5-5-5-3 in *Platecarpus*, to 5-8-8-8-6 in *Tylosaurus*.

Functional anatomy of the appendicular skeleton

The appendicular skeleton of mosasaurs is small in comparison to the overall body size, and within the limb the metapodials and phalanges are significantly longer than the propodium, epipodium, and mesopodium together (Fig. 1-4). The flat articular surfaces between the propodium and epipodium, and the rigidly-constructed mesopodium, led Russell (1967) to conclude that the only flexible joint in the limb was that between the propodium and the limb girdles. The pectoral girdle was oriented obliquely along the body wall, meaning that the forelimb was held at angle of about 45 degrees to the body axis. The shape of the proximal condyle on the humerus indicates that its motion was more dorsoventral than anteroposterior. The pelvic acetabulum faces more directly laterally than the glenoid fossa, and the hindlimb was probably held perpendicular to the body. Based on the vertically elongate shape of the pelvic girdle, Russell (1967) concluded that the muscles moving the hindlimb would have been most effective in a dorsoventral direction.

It does not seem possible that the limbs could have supported the body out of water. An exceptional specimen of *Platecarpus* preserves the fleshy portions of the limbs, showing that a paddle was formed by soft tissue, webbing between the digits and connecting widely to the body (Williston, 1899). Excepting one dissenting opinion (Lingham-Soliar, 1992b, 1999), the limbs are not considered to be a significant source of propulsion. The anatomy discussed above indicates that they were neither flexible nor muscular enough to pull the body forward in the water. It seems much more plausible that the primary propulsive organ was the tail, undulating laterally, with the limbs moving to steer and orient the body.

Chapter 1. Redescription of *Hainosaurus pembinensis* (Reptilia: Squamata) and its referral to *Tylosaurus*

Prepared for the Journal of Vertebrate Palaeontology.

REDESCRIPTION OF *HAINOSAURUS PEMBINENSIS* (REPTILIA: SQUAMATA) AND ITS REFERRAL TO *TYLOSAURUS*

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RH: BULLARD—NORTH AMERICAN *HAINOSAURUS*

ABSTRACT—*Hainosaurus pembinensis* (Reptilia: Squamata) from the Middle Campanian Pembina Member of the Pierre Shale is described in detail. Several points of anatomy are shown to be incorrect or incomplete, particularly those features that suggested an affinity with *Hainosaurus*. Many of the characters proposed by previous authors to diagnose *Hainosaurus* are shown to be inconclusive or to be shared with *Tylosaurus*. *Hainosaurus pembinensis* is referred to *Tylosaurus* because of its moderately sized suprastapedial process of the quadrate, and a lesser number of vertebrae anterior to the chevron-bearing caudals.

INTRODUCTION

Despite being named over one hundred years ago, the tylosaurine genus *Hainosaurus* (Dollo, 1885a) remains incompletely understood, especially in comparison to *Tylosaurus* itself. A series of papers by Louis Dollo (1885a, 1885b, 1887, 1890, 1904) described the type species, *Hainosaurus bernardi*, from the Early Maastrichtian Ciply Phosphatic Chalk of Belgium. Dollo (1904) also named *H. lonzeensis* for a fragmentary premaxilla and pair of caudal vertebrae from the Coniacian/Santonian of Lonzée, Belgium, though subsequent workers have considered this species a nomen dubium (Nicholls, 1988; Lingham-Soliar, 1992). Dollo's descriptions did little to diagnose *Hainosaurus* other than to ally it with *Tylosaurus*. Williston (1898:88) later remarked that no definite characteristics existed to separate *Hainosaurus* from *Tylosaurus*, except what might be found in the poorly described appendicular skeleton, and Russell (1967:176), recognising the poor preservation of the quadrates of *H. bernardi*, observed that the only "good character" to distinguish the two genera was the greater number of vertebrae anterior to the chevron-bearing caudals in *Hainosaurus*.

The first significant contribution to our understanding of the genus after Dollo's came with Nicholls' (1988) description of a new species of *Hainosaurus*, *H. pembinensis*, from the Middle Campanian Pierre Shale of Manitoba, Canada. In comparison with *H. bernardi*, Nicholls (1988:1565) was content to assign her new species to *Hainosaurus* on the basis of a higher number of vertebrae anterior to the chevron-bearing caudals, a femur longer than the humerus, a small infrastapedial process on the quadrate, and external nares relatively longer than in *Tylosaurus*.

In his review of Dollo's Belgian material, Lingham-Soliar (1992) proposed several additional anatomical features to diagnose *Hainosaurus*, including a "double buttressed" premaxillary suture and the contribution of the prefrontal to the posterior margin of the external nares. Lingham-Soliar noted that *H. pembinensis* seems to lack these diagnostic characters, but still possesses more anterior vertebrae than *Tylosaurus* (Lingham-Soliar, 1992:185).

The most recent treatment of *Hainosaurus* is that of Lindgren and Siverson (2002), who were the first to describe the dental anatomy of tylosaurines in detail. They proposed several dental features that distinguish *H. bernardi* from the species of *Tylosaurus*, and noted that *H. pembinensis* most closely resembles *Tylosaurus* in these respects. Indeed, they questioned several points of anatomy from Nicholls' (1988) description, and suggested that *H. pembinensis* may in fact be synonymous with *T. ivoensis* (Persson, 1963).

Here the material of *H. pembinensis* is redescribed with the aim of expanding and refining the anatomy of this species. Many of the questions raised by Lindgren and Siverson (2002) are confirmed and discussed. A review of the literature on *Hainosaurus* and the anatomy of *H. pembinensis* shows that many of the features used by previous authors (Dollo, 1885a; Nicholls, 1988; Lingham-Soliar, 1992) to define the genus *Hainosaurus* are at best inconclusive, and insufficient to justify the separation of *Hainosaurus* from *Tylosaurus* at a generic level. The quadrate morphology of *H. pembinensis* is robust, with an elongate, medially-deflected suprastapedial process, and a pronounced, square infrastapedial processes. This is in sharp contrast to the slender quadrate of *H. bernardi*, which seems to have very reduced suprastapedial and infrastapedial processes, but is entirely consistent with the quadrates of *Tylosaurus proriger* and *T. nepeaolicus*. I adopt a conservative approach and assign the material of "*H.*" *pembinensis* to *Tylosaurus*, at least until such a time as a useful generic diagnosis of *Hainosaurus* can be created.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **MDM**, Morden and District Museum, Morden, Manitoba, Canada; **MM**, Manitoba Museum, Winnipeg, Manitoba, Canada; **MT**, Miami Museum, Municipality of Thompson, Miami, Manitoba, Canada; **NMC**, National Museum of Canada, Ottawa, Ontario, Canada.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Linnaeus, 1758
Order SQUAMATA Oppel, 1811
Family MOSASAURIDAE Gervais, 1852
Subfamily TYLOSAURINAE Williston, 1897
Genus *TYLOSAURUS* Marsh, 1872

Type Species—*Tylosaurus proriger* (Cope, 1869).

Range—Late Coniacian to Middle Campanian.

Generic Diagnosis—See Russell (1967:171–173).

TYLOSAURUS PEMBINENSIS (Nicholls, 1988), comb. nov.

(Figs. 2-1–2-2)

Tylosaurus sp. Bardack, 1968.

Hainosaurus pembinensis Nicholls, 1988:1565, figs. 1–6.

Revised Specific Diagnosis—External nares relatively long, extending from the fourth to twelfth maxillary tooth and constituting 28-31% of skull length; postorbitofrontal overlapping prefrontal above orbit; on quadrate, suprastapedial process of moderate length, medially-deflected and tapered at its tip, infrastapedial process small, placed high on lower half of shaft; supratemporal fenestra long, constituting 24% of skull length; femur longer than humerus.

Holotype—MT 2, associated anterior portion of the skull, including the premaxilla, fragmentary maxillae, left and right pterygoids, fragmentary squamosal, basioccipital, left and right quadrates, fragmentary dentaries, left and right articulars, left surangular, right angular, left humerus, right (?) radius, right femur, disassociated phalanges, 8 cervicals (including the axis), 27 dorsals, 74 chevron-bearing caudals.

Locality and Horizon—Collected from MDM quarry 18 (North Cox Pit) in the Pembina Member of the Pierre Shale. Fossils are found in the bentonite-rich lower part of the member, correlated with the Sharon Springs Member of the Pierre Shale and the *Baculites obtusus* Zone (McNeil and Caldwell, 1981), which is assigned an earliest Middle Campanian age (Gill and Cobban, 1966; Kauffman et al., 1993).

Referred Material—MDM M73.17.02, posterior parietal fragment, fragmentary splenial, fragmentary quadrate, 7 cervicals (including an atlas neural arch), 15 dorsals, 6 caudals, and other fragments; MDM M74.01.02, squamosal, fragmentary pterygoid, left half of frontal, posterior portion of the parietal, distal femur fragment, 1 cervical, 4 dorsals, 19 caudal vertebrae, and numerous fragments. Some material remaining in jackets; MDM M74.05.06, left quadrate, lacrymal, right and left anterior surangular fragments, posterior articular fragment, ventral ilium fragment, femur, and fragmentary skull and vertebral elements; MDM M74.06.06, a composite of at least two individuals: 3 larger cervicals and an axis, 6 smaller cervicals and an axis, 3 larger anterior dorsals, and 6 smaller anterior dorsals, 8 lumbar/pygals, 28 caudals with lateral processes, and 29 caudals without lateral processes probably match the smaller of the two individuals based on their size, right quadrate, basioccipital, basisphenoid, fragmentary right pterygoid, right dentary, right surangular, right scapula, right hind limb; MDM M74.08.06/MDM M74.09.06, femur; MDM M77.03.09, anterior parietal fragment, fragmentary jaw bones, cervical vertebra and many fragments (some of which is still in jackets); MDM M77.05.07, basioccipital, right quadrate, fragmentary right maxilla, fragmentary surangular, right and left scapula, right and left coracoids, right and left humerus, right and left ulna, right (?) radius, left ilium, atlas centrum, 9 cervicals, 16 dorsals, 4 lumbars, 1 pygals, 45 caudals, 2 chevrons, ribs, and numerous fragments; MDM 77.17.07, left quadrate; MDM M83.13.18, right quadrate, other unidentified skull and jaw fragments; MM V95, nearly complete skull; NMC 40320, isolated dentary fragment.

DESCRIPTION

Almost all the referred specimens are surrounded, and often infiltrated, by gypsum crystals, which obscure surface details and in some cases distort the morphology of some elements. Descriptions have been made as accurately as possible, using multiple specimens when available.

Cranium

The only articulated skull of this taxon is MM V95. The total length of the skull, measured from the anterior tip of the premaxilla to the occipital condyle along the midline, is 1210 mm.

Premaxilla—The premaxilla is well preserved in the type specimen, though obscured by plaster at the narial margins and on the ventral surface. The premaxilla is also present in MM V95, and agrees with the type very closely. It bears two teeth in each ramus, which are broken at the base on the type and poorly preserved in MM V95, preventing a detailed description. A prominent, rectangular rostrum projects 70 mm in front of the anterior teeth on MT2. In MM V95 the rostrum is 64 mm in length, and bears on its ventral surface a pronounced, laterally elongate tubercle, as in *Tylosaurus proriger* (Russell, 1976).

The sutural contact between the premaxilla and the maxilla is poorly preserved in both specimens and difficult to trace with certainty. The internarial bar begins above the posterior edge of the fourth maxillary tooth, diverging inwards from the maxilla in a short curve before straightening. At its anterior origin the internarial bar is rectangular in cross section, with a broadly rounded base, but upon straightening the section becomes more oval. At its posterior end, the premaxilla forms an interdigitating suture with the frontal, extending for as much as half the length of the latter element (Fig. 2-1B).

Maxilla—Both maxillae are present in MT 2, though they are incomplete and heavily obscured by plaster on both their inner and outer faces. The maxilla is also preserved in M77.05.07 as two fragments of the right element, one anterior and one posterior, and as two complete elements in MM V95. The maxillary contact with the premaxilla is in the shape of a "double buttress" (sensu Lingham-Soliar, 1992), two short and rounded tongues of the maxilla extending toward the premaxilla (Fig. 2-1A). The external nares begin above the posterior margin of the fourth maxillary tooth, and extend 284 mm backward into the frontal, terminating above the twelfth tooth. Behind the premaxillary suture the dorsal rim of the maxilla is scalloped by a shallow, rounded embayment. At its posterior end, the maxilla overlaps the prefrontal with a thin tongue of bone to form the entire lateral margin of the external naris (Fig. 2-1A).

A series of anteroposteriorly elongate foramina pierce the bone above the tooth row. Ten teeth are present in the more complete left maxilla of the type, but this element is broken at the posterior end. Thirteen teeth are present in each ramus of MM V95. Teeth are poorly preserved in both of these specimens, but appear to be robust and gently recurved. Tooth crowns bear a pair of faintly serrated carinae which divide the tooth into an inflated lingual surface and a reduced buccal surface. The base of the crown is gently facetted and bears weak vertical striations.

Frontal—The most complete frontal is preserved in MM V95, but M74.01.02 contains an isolated left fragment. The frontal is a broadly triangular bone, receiving the posterior termination of the external nares in a narrowly arched embayment (Fig. 2-1B). Sutures are indistinct on MM V95, but the internarial bar of the premaxilla appears to invade the anterior frontal extensively, along as much as half the length of the element. From its anterior contact with the maxilla, the frontal expands posteriorly, becoming slightly emarginate above the orbits, and turning sharply above the postorbitofrontal to meet the parietal along a straight suture. The ventral surface bears a triangular boss immediately anterior to the frontal-parietal suture, and the olfactory canals are only shallow excavations.

Prefrontal—The prefrontal may be present in the type but it is totally obscured by plaster. It is present in MM V95, but sutures with adjacent bones are poorly preserved. The finest example is an isolated right prefrontal preserved in M74.06.06, and this is the basis for the following description. The anterior margins of the bone are scored by deep horizontal grooves, representing a loose, overlapping connection with the maxilla. The dorsal margin is flattened into a tabular surface, which bears a shallow groove anteriorly; at no point does it present a rounded surface, which would signal its contribution to the margin of the external naris. The supraorbital process is deeply excavated by a groove, as in *T. proriger* (cf. Russell, 1967:fig. 5A).

Lacrymal—Isolated triangular elements present in M74.05.06 and M74.06.06 probably represent the lacrymal. In articulation the lacrymal presented a triangular outline, with one apex of this triangle directed forwards (Fig. 2-1A). The posterior margin curves medially into the orbit. The posteroventral corner is laterally broadened into a tabular process that faces ventrally. The surface of this tabular process communicates with an oval pit on the internal face of the bone. An horizontally striated area on the anterior tip of the lacrymal presumably represents a point of overlapping articulation with the maxilla. The simply tapered anterior margin is in the form of a curve, concave posteroventrally.

Postorbitofrontal—This element is present in MM V95, but is poorly preserved. Based on the morphology of the prefrontal, the anterior process of the postorbitofrontal appears to overlap the prefrontal above the orbit.

Jugal—The only known example of this element is present in MM V95. The vertical ramus is mediolaterally compressed but anteroposteriorly broad; the jugal process of the postorbitofrontal simply overlaps it dorsally. The horizontal ramus is dorsoventrally compressed, its anterior contact with the maxilla is also simply overlapping. The posteroventral angle, formed by the diverging vertical and horizontal rami, is obtuse but rounded, and the posteroventral corner bears a slight tuberosity.

Parietal—Anterior fragments of the parietal are present in several MDM specimens: M73.17.02, M74.01.02, M74.06.06, M77.03.09. The only complete element is preserved in MM V95, but the surface of this bone is heavily damaged and many details are lost. The parietal foramen is oval and located at or very near the straight frontal-parietal suture (Fig. 2-1B). The anterior end of the parietal has limited contact with the parietal process of the postorbitofrontal. The medial body of the parietal is rectangular in outline. The suspensorial rami originate with a triangular cross section but quickly flatten dorsoventrally along their contact with the supratemporal. Poor preservation makes it unclear whether the parietal embraces the medial termination of the supratemporal with a second lateral process. The ventral surface of the parietal bears a pair of rounded projections that articulate with the supraoccipital.

Squamosal—Fragments of the squamosal are present in the type, but the best example of this bone is a complete isolated left squamosal from M74.01.02. The anterior shaft is gently arched dorsally, and bears on its dorsomedial surface a deep groove for reception of the squamosal process of the postorbitofrontal. The posterior end of the squamosal is expanded dorsoventrally. The medial face of this posterior head is roughened and bears a shallow groove for contact with the supratemporal. A triangular wing of bone is developed off the posteromedial corner to meet the suspensorial ramus of the parietal. The smooth ventral margin of the shaft curves smoothly onto the posterior head, and then recurves forward, meeting an expanded, concave articular surface for reception of the quadrate (Fig. 2-1A).

Quadrate—This diagnostic bone is represented by several elements of varying size and quality of preservation, and deserves a detailed description. Both elements are present in MT 2: the left quadrate has a fragmentary tympanic ala and has been heavily restored with plaster, and the right is badly crushed. The left quadrate is 171 mm in its maximum vertical dimension. M73.17.02 contains the ventral condyle of a large right quadrate. M74.05.06 includes a complete left quadrate, 238 mm in height. M74.06.06 contains a right quadrate, 231 mm in height, which lacks the tympanic ala. M77.05.07 preserves a beautiful right quadrate, only 160 mm tall, which lacks the tympanic rim and a portion of the adjoining ala. M77.17.07, described by Nicholls (1988) as *Tylosaurus proriger*, is a left quadrate, 193 mm in height, that agrees with the other specimens and surely belongs to the same taxon. M83.13.18 contains the dorsal fragment of a right quadrate. M77.05.07 is nearly free of encrusting gypsum and is the basis for the following description, but deviations from its form are noted at the end.

Dorsally, the main shaft of the quadrate is compressed anteroposteriorly, but ventrally it is diminished in this dimension and expanded mediolaterally to accommodate the transversely broad ventral condyle (Fig. 2-2B). The head of the shaft bears a smooth, convex condylar surface, which continues downward onto the upper surfaces of the suprastapedial process and the alar crest. The anteromedial corner of the dorsal shaft is squared off; the anteromedial edge continues as a ridge to the ventral anteromedial corner of the bone (Fig. 2-2B): this is the median ridge of Bell (1997). The dorsal half of this median ridge is rounded, while the ventral portion is narrow and accuminate.

From the squared anteromedial corner, the dorsal condyle curves downward to the posterior. Slightly behind the midpoint of the shaft, the alar crest diverges laterally and slightly anteriorly. The suprastapedial process is developed medially from the posterior edge of the dorsal shaft. The alar crest diverges obliquely laterally and posteriorly from the middle of the dorsal head of the shaft. In dorsal view the crest is parallel-sided, with a round termination. The rim of the tympanic ala is formed dorsally by the narrow posterior face of the alar crest; the anterior face is vertical and passes into the tympanic crest below. The tympanic crest originates on the lateral face of the shaft as a narrow lamina of bone, curving anteriorly to form an expanded and deeply concave conch. The tympanic rim turns ventrally after the alar crest, curving strongly laterally along the margin of the tympanic crest to its ventral corner on the lateral face of the shaft. From this ventral posterolateral corner, the tympanic rim changes direction and extends in a slightly curved line dorsomedially to terminate in a rounded prominence on the lateral face of the infrastapedial process (Fig. 2-2A); this is the posteroventral ascending tympanic rim of Bell (1997).

The posterior face of the quadrate is not extensive dorsally because of the longitudinal orientation of the shaft. The suprastapedial process dominates the upper third of the shaft, in posterior view, with the infrastapedial process developed toward the top of the lower half. The suprastapedial process is of moderate length (not reaching the infrastapedial process), though little of this length is visible in lateral view because of its strongly medial orientation (Fig. 2-2A). From the posterior edge of the quadrate shaft, the suprastapedial turns abruptly to face directly medially, and ventrally at about 45 degrees. The dorsal surface is convexly rounded and smooth, a continuation of the dorsal condylar surface. This smooth surface curves downward to cover most of the anterior face of the process, but extends only a short distance onto the posterior face. In posterior view, the suprastapedial process is convexly arched along its dorsal margin, while its ventral margin is irregular (Fig. 2-2D). The ventral margin is continuous with the acuminate edge of the tympanic rim, and is likewise developed into a thin crest. The posterior face of the process is concave between the smooth condylar surface and thin ventral edge; the roughened surface of this concavity represents the origin of part of the M. depressor mandibulae (Callison, 1967:9, fig. 9; Russell, 1967).

The meatal notch is square in outline when viewed laterally (Fig. 2-2A). Its ventral border is formed by a prominent infrastapedial process which extends obliquely posteriorly and medially from the posterior shaft. In mediolateral view, the outline of the infrastapedial process is rounded. In posterior view, its medial outline is sinusoidal and its lateral outline slightly concave (Fig. 2-2D). This is the result of a lateral curvature of the distal tip. The outer, posterior margin curves around this deflection and continues ventrally onto the face of the shaft as a low, curving ridge which fades before the reaching the ventral condyle.

The medial face of the shaft is flat and longitudinal dorsally, but with the rotation of the shaft at mid-height turns to face obliquely posterior. The stapedial pit is located toward the upper third of the medial shaft; it is rectangular in outline, with a length-to-width ratio of about 3.5:1 (Fig. 2-2C).

The outline of the ventral condyle is sinusoidal in anteroposterior aspect (Fig. 2-2B). In ventral view the smoothly polished surface of the condyle is irregular in shape. The anteromedial corner is pinched out, conforming to the acuminate medial edge of the ventral shaft. The rim of the condyle curves posteriorly, then follows the flat posterior face in a nearly straight line, but climbs to nearly meet the tympanic rim on the lateral edge of the bone. The rim of the condyle is deflected dorsally onto the anterior face at a point slightly lateral to the midpoint of the shaft.

The largest quadrates, M74.06.06 and M74.05.06, differ from M77.05.07 mainly in being more robust. The tympanic ala of the type's left quadrate originates higher on the shaft than in other specimens, giving the whole element a question-mark shape in lateral profile (see Nicholls, 1988:fig. 1). This morphology is misleading, however, because the ala is broken through the alar crest and the bone edges show that it has been restored incorrectly. The tympanic rim is present on the left quadrate of MT2, but it is joined with plaster and its original orientation cannot be determined. The infrastapedial process of the quadrate of M74.05.06 comes to a sharp point, being triangular in lateral view, whereas the infrastapedial of M74.06.06 is even more broadly rounded than M77.05.07. The infrastapedial of M77.17.07 is prominent and square. The suprastapedial process of M74.05.06 is unusual in that it extends ventrally to the medial side of the infrastapedial process.

Pterygoid—Both pterygoids are complete in MT 2. M74.06.06 and M74.01.02 contain anterior fragments of the right element. It bears ten teeth, diminishing slightly in size from front to back, in a sinuous row on the ventral surface. These teeth are relatively smaller than the marginal dentition and more recurved, with a circular cross section and gently striate enamel.

Basioccipital—The basioccipital is known from isolated bones contained in MT 2, M74.06.06, and M77.05.07. The medullary cavity has straight margins, and is not ornamented along its floor. The basal tubera are horizontally broad, not tapering distally, and bear roughened, curved articular surfaces on their extremities. The tubera are directed ventrolaterally, making an angle of 45 degrees with horizontal.

Basisphenoid—M74.06.06 includes the only known element, which is not sufficiently well preserved to admit details of nerve and blood vessel foramina in the sella turcica. The posterior end of the bone is square, but on the ventral margin bears two round, concave flanges that overlap the basal tubera of the basioccipital. The alar process is broken on both sides, but could not have been extensive. The basipterygoid processes are horizontally broad and oriented anterolaterally.

Dentary—Both dentaries are present in MT 2, though the left is abbreviated at its posterior end and both are covered heavily by plaster on their medial and dorsal surfaces. MM V95 preserves both dentaries completely. M74.06.06 contains a right element, which is missing the posteriormost portion. The dentary bears an edentulous, rectangular rostrum in front of the first tooth. The dorsal and ventral margins of the bone are only slightly curved. Anteroposteriorly elongate foramina are present along the length of the alveolar margin.

In the type there are twelve teeth present in the complete right ramus, ten in the left. There are twelve teeth in each ramus in MM V95. As observed by Nicholls (1988), the dentary of M74.06.06 preserves 13 teeth rather than 12. Teeth are poorly preserved in all specimens: the type dentaries have both had their teeth restored, either replaced or reattached by plaster, in M74.06.06 and MM V95 the teeth are either missing or fragmentary. Tooth morphology appears to match that of the maxillary teeth.

Splenial—M73.17.02 preserves both splenials, both posteroventral fragments. The articular surface for the angular is elliptical in outline when viewed from the posterior; this surface is concave and bears a raised ridge which extends from the center of the articular surface dorsomedially to the margin.

Angular—MT 2 contains both angulars, though neither is complete or well preserved. Little can be determined about this element, other than that the articular surface for the splenial is semitriangular in outline, with one apex pointing ventrally.

Surangular—MT 2 includes a nearly complete left surangular, M74.06.06 contains a right element, M74.05.06 anterior fragments of both bones, and M77.05.07 a posterior fragment of the left element. In all these examples the medial face of the bone is poorly preserved. The surangular is a large, rectangular bone. The anterior margin is heavily striated, and bears a deep dorsal sulcus for reception of the coronoid. The remainder of the dorsal margin is smooth and nearly straight. The posterior end forms the front half of the glenoid fossa, a smoothly concave, hemispherical articular surface, which faces obliquely dorsomedially and posteriorly.

Articular—Both articulars are preserved in MT 2, and a posterior fragment is present in M74.05.06 confirming this morphology. The anterodorsal face of the articular forms the posterior half of the glenoid fossa, a smoothly concave hemispherical articular surface, which faces obliquely dorsomedially and anteriorly. Behind the fossa, the articular extends posteriorly and slightly medially to form the retroarticular process. In lateral outline this process is strongly curved along its dorsal margin, with a nearly straight ventral border that is oriented obliquely posteroventrally (Fig. 2-1A).

Appendicular Skeleton

Scapula—Both scapulae are present in M77.05.07, and the left scapula in M74.06.06. The scapula is a robust and elongate bone, though only half the area of the coracoid. The ventral edge of the bone bears a pair of smooth, oval articular surfaces, an anterior, ventrally-facing coracoid facet and a posterior, posteroventral-facing glenoid facet. The scapula is constricted immediately above these articular surfaces, but expands again into a mediolaterally compressed blade. The anterior coracoid facet merges directly into a roughened and unfinished margin representing the point of attachment of a large cartilaginous suprascapula (Osborn, 1899). This margin continues completely around the anterior and superior borders, inscribing nearly 270 degrees of revolution about the center and terminating well behind the glenoid facet. A smooth and nearly straight posterior margin finishes the bone's circumference. The medial face of the bone is slightly concave in both planes, the lateral face slightly convex vertically. Radial striations cover the bone's margins on both sides.

Coracoid—M77.05.07 preserves both coracoids. The dorsal head bears a pair of smooth, oval articular surfaces: an anterior scapular facet that faces dorsally and a posterior glenoid facet that faces posterodorsally. Below the head the coracoid constricts slightly; this neck is pierced anteriorly by a circular foramen marking the passage of the nerve for the M. supracoracoideus (Russell, 1976:85). Medially the bone continues to flatten dorsoventrally, the anterior edge remaining thicker than the posterior, but expands again transversely into an elongate fan. The anterior margin of this fan is straight, while the posterior margin is strongly concave, but these margins are nearly equal in length. The medial margin is roughened but entire, without even the notch that is occasionally present in *Tylosaurus* (Osborn, 1899: fig. 9).

Humerus—MT 2 preserves a single humerus, while M77.05.07 preserves both elements; these bones are nearly the same length and are very similar in form. The humerus is an elongate bone, though only 196 mm long in MT2. The condyles are unfinished and would have been capped by thick cartilages in life. The proximal head is expanded anteroposteriorly, to nearly the same width as the distal head. The proximal surface cannot be differentiated into a glenoid condyle and postglenoid process, together they form a semitriangular and slightly convex surface on the proximal end of the shaft. The deltoid tuberosity is a flat oval surface which faces anterodorsally and is separated from the glenoid condyle by a slight constriction. The pectoral crest is large and placed slightly forward on the ventral face of the shaft. The bone constricts towards the midpoint of the shaft, but expands again anteroposteriorly, forming strongly flexed anterior and posterior margins. The distal end is as undifferentiated as the proximal, forming a single roughened surface. A small ectepicondyle and larger entepicondyle are present as proximal flexions of the distal surface. The distal surface has its greatest width across the radial facet. The bone narrows behind, expanding again into the entepicondyle. A shallow ectepicondylar groove is present on the anterodorsal edge of the distal surface.

Radius—The radius is known from isolated elements preserved in MT 2 and M77.05.07. It is an elongate bone. The proximal and distal articular facets are both elliptical in outline, their surfaces roughened and slightly concave. The middle of the shaft is constricted, primarily longitudinally, making both anterior and posterior margins concave.

Ulna—Both ulnae are present in M77.05.07. Like the radius, this is an elongate element, but more slender and less expanded proximally and distally.

Ilium—The ilium is known from a ventral fragment in M74.05.06 and a complete left bone in M77.05.07. The ventral head of the ilium bears an oval articulation, the surface of which is convex and slightly roughened, facing ventrolaterally. Dorsal to the head, the shaft constricts and curves gently to the anterior before straightening for the remainder of its length. The dorsal tip is abrupt and square.

Femur—The femur is represented in several specimens: MT2, M74.01.02, M74.05.06, and M74.08.06/ M74.09.06. It is an elongate bone, 216 mm long in the type, and expanded at both ends. As in the humerus, the roughened and unfinished proximal and distal surfaces would have been covered by cartilage. At the proximal end the subcircular surfaces of the glenoid condyle and internal trochanter are continuous. The internal trochanter is placed well forward on the anteroventral corner of the proximal head. The shaft constricts towards the middle of the bone, expanding again anteroposteriorly so that the distal end is broader than the proximal. The tibial and fibular facets form a continuous oval surface, though the fibular facet is deflected proximally.

Vertebral Column

Terminology—Russell (1967) divided the caudal series of mosasaurs into three regions: a short anterior region where the vertebrae have transverse processes but lack haemal arches called the pygal region, a transitional region with transverse process and haemal arches called the intermediate region, and a posterior region lacking transverse processes called the terminal series. Nicholls (1988) used 'terminal' to describe a short series of 5 vertebrae in the type that seemingly lacked both transverse processes and haemal arches, but this was not Russell's usage of the term. Similarly, she used 'precaudal' to include all vertebrae anterior to the first chevron-bearing caudal, or the first intermediate caudal, but this excluded the pygals, which are part of the caudal series.

Cervical Vertebrae—The atlas is incompletely known from a neural arch in M73.17.02 and a centrum in M77.05.07. On the neural arch the synapophysis is present only as a small tuberosity on the posterior margin. The spinous process is short, less than two-thirds of the vertical height of the main body of the neural arch. The axis is present in MT 2, not missing as reported by Nicholls (1988:1565), and M74.06.06 (where there are actually two), but in both cases only the centrum is present, the neural arch and processes absent. The axis is a massive vertebra, its posterior articular surface is convex and circular in outline. Cervicals behind the axis have a horizontally oval centrum in posterior view, with a width to height ratio of about 1.25:1. Zygosphenes and zygantra are absent. The hypapophyses articulate with a circular facet on the posteroventral surface of the cervical centrum. In MT 2, six cervical vertebrae—including the atlas and axis—bear functional hypapophyseal articulations on their ventral surfaces, and an additional three more bear traces of the articulation as a tubercle of declining height. The hypapophyses are conical, and flexed posteriorly.

The end of the cervical series can only be located by identifying the first rib with a connection to the sternum (Romer, 1956), and very few mosasaur specimens are complete enough to allow this determination. Osborn (1899) reported seven cervicals from a beautiful articulated skeleton of *Tylosaurus*, and Williston (1910) the same for *Platecarpus*. In both these genera there are also six hypapophysis-bearing cervicals, which makes it tempting to conclude that there are seven cervicals in *T. pembinensis*. Dollo's (1887:513) report of ten cervicals in *H. bernardi* was not discussed or corroborated by Lingham-Soliar (1992), and is difficult to confirm from published figures. Certainly, Nicholls' (1988) assignment of nine cervicals to *T. pembinensis* was not based on an articulated costal series, and so must be treated with caution.

Dorsal Vertebrae—MT 2 preserves 29 vertebrae after the cervical series and before the first chevron-bearing caudal. Zygopophyses are present only on the first eight dorsal vertebrae, but are poorly developed and decline throughout this series. Anterior dorsals have horizontally oval condyles like the cervicals; backward in the column they gradually become triangular, with one apex of the triangle pointing dorsally. The end of the dorsal series and the beginning of the caudal series is determined by locating the last thoracic rib, but in MT 2 most of the synapophyses are broken and the ribs absent. This makes it impossible to differentiate the series of vertebrae anterior to the chevron-bearing caudals, and so dorsals and pygals have been included together in a morphologically similar series of 29 indeterminate vertebrae.

Caudal Vertebrae—Assuming that some pygals are present towards the end of the series of indeterminate vertebrae in MT 2, these caudals are very similar in shape to the posterior dorsals. The centra are triangular in cross section. The first definite caudal vertebrae are those with chevron articulations. Chevrons are not fused to their centra. MT 2 preserves 74 caudal vertebrae bearing chevron articulations on their ventral surface, the first 32 of which bear lateral processes, followed by 42 terminal vertebrae. The centra of anterior chevron-bearing caudals are roughly triangular, but posteriorly in the column become laterally compressed and rectangular in outline.

A series of 26 small vertebrae is present in the caudal series of MT 2. Well-developed zygopophyses distinguish these vertebrae from the surrounding caudals, and an absence of hypapophyses identifies them as dorsal vertebrae (Fig. 2-5). The diameter of their centra is considerably less than that of the preceding dorsals (around 60 mm vs. 100 mm); these vertebrae are evidently part of a smaller mosasaur that was either found associated with MT 2, or accidentally included with it after field collection.

DISCUSSION

Morphology

Prefrontal—Lingham-Soliar (1992) stated that the prefrontals of *H. bernardi* are "very poorly preserved," and while their apparent borders with the adjoining bones are similar to those of *Tylosaurus* and "*H.*" *pembinensis*, a slender process of the prefrontal forms a portion of the narial margin (Lingham-Soliar 1992:176). This condition is common to many mosasaurs, but differs from that of *Tylosaurus*, in which a process of the maxilla continues posteriorly to overlap the prefrontal along the lateral margin of the nares. Published figures of the prefrontal of *H. bernardi* give no indication of the condition of this element, nor is its poor preservation likely to provide a smoothly finished surface that would demonstrate involvement in the narial margin. The maxillae are unlikely to resolve this uncertainty, as Lingham-Soliar's (1992:175) description made no mention of their posterodorsal extremity. In light of these concerns, it would seem that a focussed examination of the two IRSNB specimens is required to determine whether prefrontal contribution to the narial margin is a difference between *Tylosaurus* and *H. bernardi*.

External Nares—In *Tylosaurus* the position of the external nares is an important diagnostic character: in *T. proriger* the nares begin above or slightly behind the fourth maxillary tooth, while in *T. nepaeolicus* they begin between the third and fourth tooth (Russell, 1967). In *T. pembinensis* the nares begin above the fourth maxillary tooth and extend back as far as the twelfth tooth (Fig. 2-1, Fig. 2-4). Dollo (1885b) measured the external nares of *H. bernardi* at 430 mm, 28% of the total skull length. Lingham-Soliar (1992:173) confirmed this percentage in his specific diagnosis ("28-31%"), but on the photograph of the type (Lingham-Soliar, 1992:pl. 1) and reconstruction of the skull (Lingham-Soliar, 1992:fig. 3) the nares appear shorter, about 24% of total skull length. This is consistent with the length of the nares reported for *Tylosaurus* (Russell, 1967:18), and so this character cannot be used to diagnose *Hainosaurus*.

Teeth—Dollo (1885a) observed three distinct tooth morphologies in *H. bernardi*: (1) teeth with a circular section and a single carina; (2) teeth with a more compressed section and two carinae; and (3) teeth resembling (2) but being more 'flattened.' Lingham-Soliar (1992) observes that anterior dentary teeth of *H. bernardi* have a single anterior carina, while posterior teeth have two carinae, but does not reconcile Dollo's descriptions with this morphology. Nicholls (1988) stated that teeth of *T. pembinensis* do not exhibit the kind of heterodonty observed by Dollo (1885a). Heterodonty in the marginal dentition would not be unexpected, given that anterior teeth of mosasaurs often have a morphology distinct from that of posterior teeth, but this is very difficult to verify given the poor preservation of the Morden tooth material. Lindgren and Siverson (2002) noted that tooth crowns of *H. bernardi* are bucco-lingually compressed and symmetrical: the teeth of *T. pembinensis* match those of the other species of *Tylosaurus*, having a more circular cross section and an inflated lingual face. The teeth of *T. pembinensis* and *T. ivoensis* are so similar that Lindgren and Siverson (2002) have suggested the synonymy of the two species.

Vertebral Column—Nicholls (1988) reported 63-64 vertebrae anterior to the first chevron-bearing caudal in MT 2. This included a reconstruction of 9-10 cervical vertebrae: 7 preserved, with the atlas, axis, and potentially another anterior cervical missing. As previously mentioned, there is no justification for a cervical count without articulated ribs. Nicholls may have been attempting to reconcile her observations with Dollo's (1887) report of 10 cervical vertebrae in *H. bernardi*, given that this was a new species of the same genus. The axis centrum is certainly present in MT 2 and the author observed no drastic shift in size which would indicate the absence of an intervening cervical. It is thus with confidence that I report 6 hypapophysis-bearing cervicals and conservatively estimate 7 cervicals based on exceptionally complete skeletons reported by previous authors (Williston, 1898; Osborn, 1910).

Nicholls (1988) observed 54 vertebrae in the dorsal and pygal regions (33 dorsals and 21 pygals). I report only 29 from this region, without differentiating the two for reasons of uncertainty. The 26 dorsal vertebrae within the caudal series definitely represent another specimen, and are probably not even from the same species: the degree of development and extent of the zygopophyses are greater than those of the preceding dorsal vertebrae of MT2 (Fig. 2-5). *Platecarpus*, the most common Pembina mosasaur, is a likely culprit. It is evident that Nicholls (1988) included these vertebrae within the dorsal-pygal series in her tally, as my enumeration of the remaining caudal series matches exactly (Table 2-1). Removing these foreign vertebrae brings the number of vertebrae in the dorsal-pygal region down to 28. Accounting for the missing atlas, this makes the number of 'precaudals' 36, exactly as reported in *Tylosaurus* by Williston (1898). Nicholls' (1988) report of 39 'precaudals' in M74.06.06 and 47 in M77.05.07 is also erroneous. In M74.06.06, I counted only 26 'precaudals' and 57 caudals, but the presence of two axes of very different diameters demonstrates that this specimen is a composite of at least two individuals, and without more vertebrae it is impossible even to be sure which caudals belong with which 'precaudals.' A cursory inspection of the vertebrae of M77.05.07, in which they were not removed from their drawers and articulated to be certain of identifications, recognised only 30 'precaudals.' Regardless of the exact number in these additional specimens, I do not believe it exceeds 36.

Table 2-1 summarises this reinterpretation of the vertebral formula. Removal of the foreign dorsal vertebrae reduces the total number of 'precaudal' vertebrae to 36 from 63–64. *Tylosaurus* is reported to have 35–37 vertebrae anterior to the chevron-bearing caudals (Russell, 1967). Dollo (1887) observed 49 'precaudals' in *H. bernardi*, and 98 vertebrae in total, admitting that the vertebral column was probably incomplete. Lingham-Soliar (1992) identified half of Dollo's pygal series as dorsals; this does not change the total number of 'precaudals,' though he reported that an undetermined number of pygals are missing (Lingham-Soliar, 1992:173). Regardless of the exact number present in *H. bernardi*, the vertebral formula of the Morden material resembles that of *Tylosaurus* rather than *Hainosaurus* as it is currently understood.

Nicholls (1988) correctly observed that in *T. pembinensis* the articular faces of cervical centra are transversely oval in outline, while those of the other *Tylosaurus* species are "more nearly circular" (Russell, 1967:76). This is a difference of semantics rather than morphology; published descriptions of the vertebrae of Kansas species of *Tylosaurus* show that the vertebrae have a width-to-height ratio of about 1.2:1, much like that of *T. pembinensis* (Williston, 1898). The cervicals of *H. bernardi* have also been described as 'nearly circular,' but a photograph shows that the articular face is considerably wider than it is tall, and also matches *T. pembinensis* very closely (Lingham-Soliar, 1992:pl. 5C). There does not appear to be a significant difference between these tylosaurine species in the shape of the cervical centra.

Taxonomy

Generic Diagnosis—Nicholls' (1988:1565) diagnosis of the genus *Hainosaurus* was as follows: (1) rectangular edentulous rostrum on premaxilla and dentary; (2) 12 teeth in maxilla, 12-13 in dentary; (3) external nares relatively longer than in *Tylosaurus*; (4) frontal excluded from the orbit by prefrontal-postorbitofrontal contact; (5) suprastapedial process of quadrate short, infrastapedial process "reduced to small swelling half-way up quadrate shaft;" (6) scapula much smaller than coracoid, coracoid not notched; (7) femur longer than humerus; (8) 63–64 vertebrae anterior to chevron-bearing caudals; and (9) adult body size very large, estimated length 12–15 m.

Character 1 is equally present in *Tylosaurus*, and the premaxillary rostrum is a defining feature of all tylosaurines. Character 2 falls within the range of Russell's (1967:171) definition of *Tylosaurus*: 12–13 teeth in maxilla, 13 in the dentary. As discussed above, character 3 appears to be unique to *T. pembinensis*, but not to *Hainosaurus*. Character 4, contact between the prefrontal and postorbitofrontal excluding the frontal from the dorsal orbital margin, is present in *Tylosaurus* and other mosasaur genera. Character 5 is, as I have hopefully demonstrated, an inadequate description of the morphology of the quadrate. The suprastapedial process is short in comparison with other mosasaur genera, but comparable to that of *Tylosaurus* and much larger than in *H. bernardi*. The infrastapedial is more than a mere 'swelling.' Character 6 describes a typically tylosaurine condition, in which the scapula is smaller than the coracoid; the coracoid notch is variably present in *Tylosaurus* (Russell, 1967). Character 8 is an incorrect description of the vertebral formula in *T. pembinensis*: the number of 'precaudals' is significantly less than this number, and falls within the range of

Tylosaurus (Table 2-1). It does appear, however, that *H. bernardi* possesses significantly more 'precaudal' vertebrae (Table 2-2). Character 9, while descriptive, should not be taxonomically diagnostic, and large specimens of *T. proriger* have been observed within this size range (Everhart, 2002).

Lingham-Soliar (1992) listed many anatomical features in his diagnosis of *Hainosaurus*, but most are equally attributable to *Tylosaurus* and some to other mosasaurs. The remaining characters include: (1) a 'double buttressed' premaxillary suture, and (2) the contribution of the prefrontal to the posterior margin of the external nares. Character 1 is observable in specimens of *Tylosaurus* (pers. obs.), to an equal or lesser extent than described by Lingham-Soliar (1992); this feature could have some utility, but requires a more precise definition. As discussed above, the poor preservation of the prefrontal and posterior maxilla in the material of *H. bernardi* makes the validity of character 2 uncertain. Posteriorly directed, ventral processes of the premaxilla in *H. bernardi*, stated to be undescribed in the Tylosaurinae (Lingham-Soliar, 1992:175), have been observed in *Tylosaurus* by Williston (1898:104, pl. XVIII), in *Taniwhasaurus* by Caldwell et al. (2005:396, fig. 5), and the base of this process is evident in Russell's (1967:fig. 2) figure of the premaxillae.

Lindgren and Siverson (2002) provided an informal diagnosis of *Hainosaurus* that is nonetheless the best to date: (1) marginal tooth crowns are more bucco-lingually compressed, giving the tooth a more symmetrical cross section, (2) carinae on marginal tooth crowns are well developed, (3) carinae on pterygoid teeth are serrated, (4) the suprastapedial process of the quadrate is small, (5) the infrastapedial process of the quadrate is barely present, (6) the quadrate has a rectangular profile in lateral view, (7) femur is longer than the humerus, (8) greater number of vertebrae anterior to the chevron-bearing caudals, and (9) anterior intermediate caudal centra are wide and short. From what little has been published on dental anatomy, characters 1–3 appear to characterise the teeth of *H. bernardi*. Characters 4–6 describe the smaller suprastapedial process, infrastapedial process, and tympanic ala of the quadrates of *H. bernardi* compared to the species of *Tylosaurus*. The quadrate of the newly described *Tylosaurus kansasensis* (Everhart, 2005) also has a reduced infrastapedial process, but, taken together, this suite of features characterises the quadrate of *Hainosaurus*. Characters 7 and 8 have been retained from Nicholls (1988). The utility of character 9 cannot be determined in the absence of good vertebral descriptions of *H. bernardi*.

Specific Diagnosis—Nicholls' (1988:1566) definition of "*H.*" *pembinensis* was as follows: (1) homodont marginal dentition; (2) supratemporal fenestra relatively longer than in *H. bernardi*; and (3) suprastapedial process of quadrate present. As stated previously, the homodonty of the marginal dentition is difficult to confirm given the preservation of tooth crowns in the Morden material. Dollo (1885b) reported the length of the supratemporal fenestra in *H. bernardi* as 300 mm, 19% of the total skull length, and this is supported by Lingham-Soliar's (1992) figures. This matches the condition in *T. proriger* (Russell, 1967:fig. 92), and thus the greater length of the supratemporal fenestra in *T. pembinensis* (Fig. 2-4) is unique to the species. The quadrate of *H. bernardi* was described by Dollo (1885a; 1885b) as lacking a suprastapedial process, but photographs of this element show that one is present, though much reduced in size compared to that of other mosasaurs (Lingham-Soliar, 1992:fig. 9).

CONCLUSIONS

In nearly all anatomical features, these specimens are consistent with the described species of *Tylosaurus*. The quadrate in particular resembles that of *T. proriger*, having a robust infrastapedial process about one-third up the height of the quadrate, suprastapedial process of moderate size, well-developed tympanic ala, and rectangular stapedial pit. The quadrate of *H. bernardi* has a smaller suprastapedial process and an incipient infrastapedial; the tympanic ala is much shallower. *H. bernardi* certainly has more vertebrae anterior to the chevron-bearing caudals. A number of other anatomical features, such as contribution of the prefrontal to the narial margin and a heterodont dentition, may prove to distinguish *Hainosaurus* from the species of *Tylosaurus*, but only after they have been conclusively demonstrated from the type material.

Dollo's second species of *Hainosaurus*, *H. lonzeensis*, has been regarded as a nomen dubium by Nicholls (1988) and Lingham-Soliar (1992) because it consists of a fragmentary premaxilla and two terminal caudals, and so lacks their diagnostic ✓ characters. Lindgren and Siverson (2002) agreed with these authors, but noted that nearly 50 isolated tooth crowns from the type locality were similar to those of *T. proriger*. The preservation of the type does not seem to allow taxonomic assignment beyond the level of the Tylosaurinae.

The assignment of *Mosasaurus gaudryi* Thévenin, 1896, to *Hainosaurus* has been justified by prefrontal-postorbitofrontal contact above the orbit, the large size of the skull (Bardet, 1990) and a 'double-buttressed' premaxillary suture (Lingham-Soliar, 1992). As discussed above, none of these characters is diagnostic of *Hainosaurus*. Bardet's (1990) third character, the ratio between the length of the external nares and the length from the parietal foramen to the premaxillary rostrum, can no longer be defended given the assignment of "*H.*" *pembinensis* to *Tylosaurus*. This confirms Lindgren and Siverson's (2002) doubts about the validity of this species. The premaxillary rostrum clearly identifies Thévenin's type as a tylosaurine, but "*Mosasaurus*" *gaudryi* cannot be assigned to *Hainosaurus* as it is current understood.

It should be clear from much of the earlier discussion that a formal diagnosis of *Hainosaurus* is lacking. The generic diagnoses of Nicholls (1988) and Lingham-Soliar (1992) are unsatisfactory, given that in most characters they cannot distinguish *Hainosaurus* from *Tylosaurus*. A detailed description of the two known specimens of *H. bernardi* is warranted, and should resolve much of the confusion that currently surrounds the genus.

The specific diagnosis of *T. pembinensis* given in the taxonomic section has been distilled from Nicholls' (1988) generic and specific diagnoses. Like *T. proriger*, the postorbitofrontal overlaps the prefrontal laterally above the orbit. The quadrates of *T. pembinensis* most resemble those of *T. proriger*, but have a more medially-deflected suprastapedial process (Fig. 2-2). The infrastapedial process is larger than in *T. kansasensis*, and unlike *T. nepaeolicus* it is placed high on the lower half of the shaft. The external nares (Fig. 2-4) and supratemporal fenestra are considerably longer than in other known tylosaurines. The femur is longer than the humerus. These differences do not seem to be of a generic order, but are sufficient to justify the retention of "*H.*" *pembinensis* and assign it to *Tylosaurus*. This designation seems prudent given the many uncertainties in our understanding of the genus *Hainosaurus*, though I have every expectation that a rigorous examination of *Hainosaurus* may allow *T. pembinensis* to be reassigned in the future. Synonymy of *T. pembinensis* and *T. ivoensis*, as suggested by Lindgren and Siverson (2002), is perhaps premature given how little is known about the anatomy of *T. ivoensis* aside from associated teeth and vertebrae.

The assignment of "*H.*" *pembinensis* to *Tylosaurus* means that, disregarding Nicholls' (1988) erroneous reference of M77.17.07 to *T. proriger*, there are now two occurences of *Tylosaurus* known from the Middle Campanian of the Western Interior Seaway: *T. proriger* from the lower Pierre Shale of South Dakota, and *T. pembinensis* from the lower Pierre Shale of Manitoba. The presence of large species of *Tylosaurus* coexisting as closely as South Dakota and southern Manitoba, both of which are within the Northern Interior biogeographic subprovince of Nicholls and Russell (1990), would seem contrary to expectations, but we now know that *T. kansasensis* and *T. nepaeolicus* existed together in the lower Smoky Hill Chalk (Everhart, 2005). The osteological differences between *T. pembinensis* and described specimens of *T. proriger* from the Kansas Niobrara are unavoidable, even if they are not as great as once thought.

The difficulties in understanding tylosaurine systematics arise from the morphologically conservative nature of the Tylosaurinae across a Late Coniacian to Early Maastrichtian time span. Researchers need to examine old and new collections with an appraising eye to gain an understanding of these mosasaurs.

ACKNOWLEDGMENTS

The author thanks Mike Wadell, and the other staff and volunteers of the Morden and District Museum for granting access to the material, and for their assistance and hospitality while in Morden; Jim Woods of the Miami Museum for access to the holotype, and John Andrews for sharing his knowledge of the specimen; Dr. Graham Young of the Manitoba Museum for access to MM V95; Gilles Danis and the staff of PAST for access to MDM M74.06.06 in their shop, as well as very generously creating casts of some of the more important elements. The Natural Science and Engineering Research Council of Canada provided funding for much of this project.

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TABLE 2-1. Vertebral counts of MT 2 compared between Nicholls (1988) and this manuscript. Note that the vertebral totals are identical, but the distribution of vertebrae within each region of the column is different. CBC denotes chevron-bearing caudals, and 'terminals' is used here in the sense of Nicholls (1988), not Russell (1967).

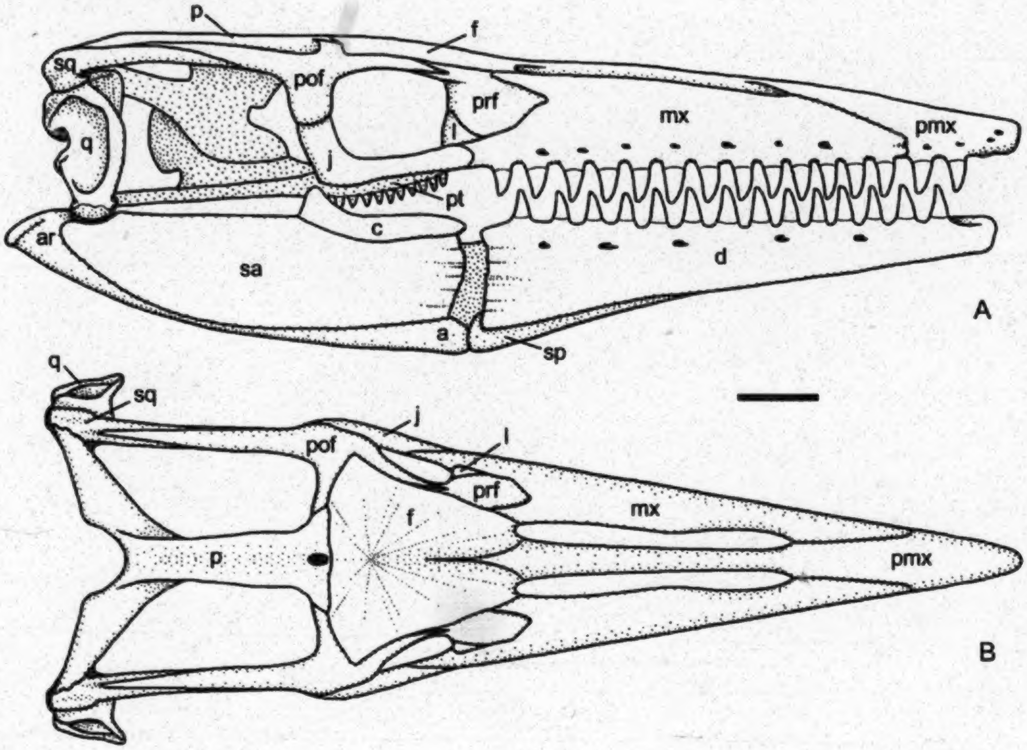
Region	Nicholls (1988)		Here	
	Observed	Reported	Observed	Reported
Cervical	7	9-10	6	7
Dorsal	33	33	29	29
Pygal	21	21		
CBC	69	69	69	69
'Terminal'	5	5	5	5
Foreign	-	-	26	26
Total	135	137-138	135	136

TABLE 2-2. Comparison of vertebral formulae in tylosaurine mosasaurs.

	T. pembinensis	*H. bernardi* (Dollo, 1887)	*H. bernardi* (Lingham-Soliar, 1992)	*Tylosaurus* (Russell, 1967)
Cervicals	7	10	40	7
Dorsals	29	19		22-23
Pygals		20	>9	6-7
Precaudals[†]	36	49	>49	36-37
Caudals[†]	74	49	>68	89-112
Total	110	>98	>117	125-149

[†] 'Precaudals' are defined as those vertebrae anterior to the first chevron-bearing caudal, and 'caudals' as the vertebrae posterior to, and including, the first chevron-bearing caudal.

FIGURE 2-1. The reconstructed skull of *Tylosaurus pembinensis*, from the Middle Campanian Pierre Shale of Manitoba, based on MM V95. **A,** lateral view. **B,** dorsal view. **Abbreviations**: **a,** angular; **ar,** articular; **c,** coronoid; **d,** dentary; **f,** frontal; **j,** jugal; **l,** lacrymal; **mx,** maxilla; **p,** parietal; **pmx,** premaxilla; **pof,** postorbitofrontal; **prf,** prefrontal; **pt,** pterygoid; **q,** quadrate; **sa,** surangular; **sp,** splenial; **sq,** squamosal. Scale bar equals 100 mm.


p
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mx
f
p
pmx
B

FIGURE 2-2. The reconstructed quadrate of *Tylosaurus pembinensis*, based on MDM M77.05.07. **A**, lateral view. **B**, anterior view. **C**, medial view. **D**, posterior view.

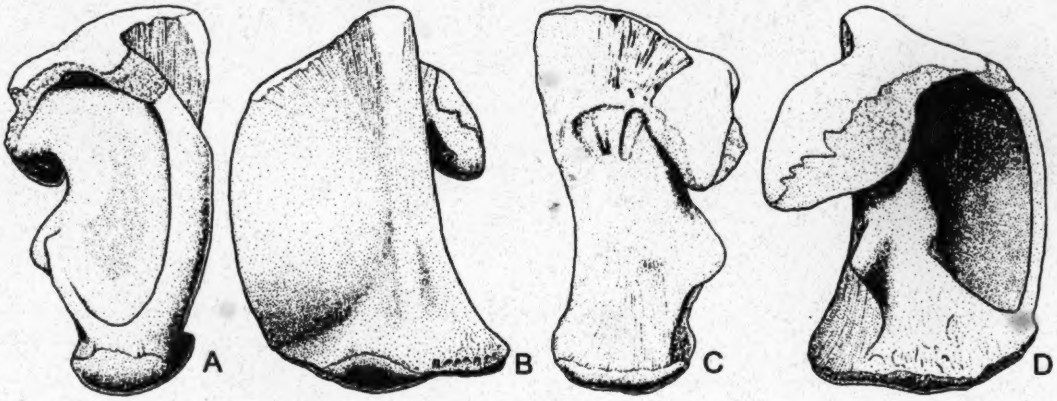
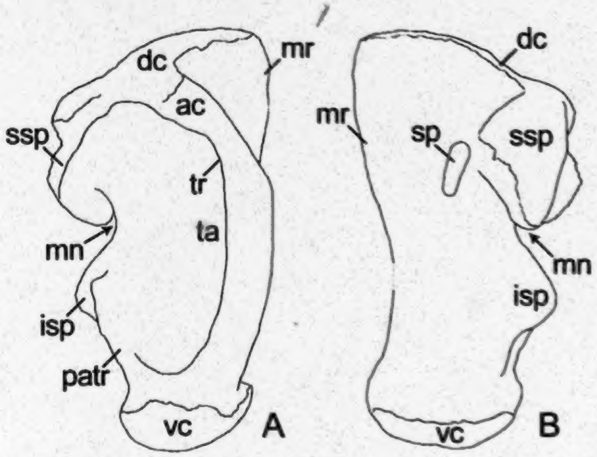


FIGURE 2-3. Summary of anatomical landmarks on the mosasaur quadrate used in the text. **A**, lateral view. **B**, medial view. **Abbreviations: ac**, alar crest; **dc**, dorsal condyle; **isp**, infrastapedial process; **mn**, meatal notch; **mr**, median ridge; **patr**, posteroventral ascending tympanic rim; **sp**, stapedial pit; **ssp**, suprastapedial process; **ta**, tympanic ala; **tr**, tympanic rim; **vc**, ventral condyle.


dc
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ac
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A
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B

FIGURE 2-4. Extent of the external narial opening in tylosaurine species, expressed in terms of maxillary tooth position. Data for *Tylosaurus* species from Russell (1967), for *Hainosaurus bernardi* from Lingham-Soliar (1992:fig. 3).

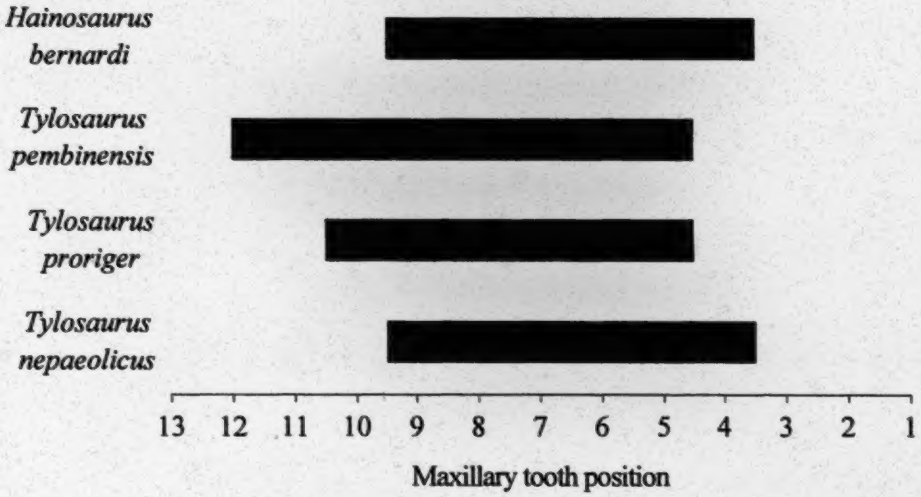
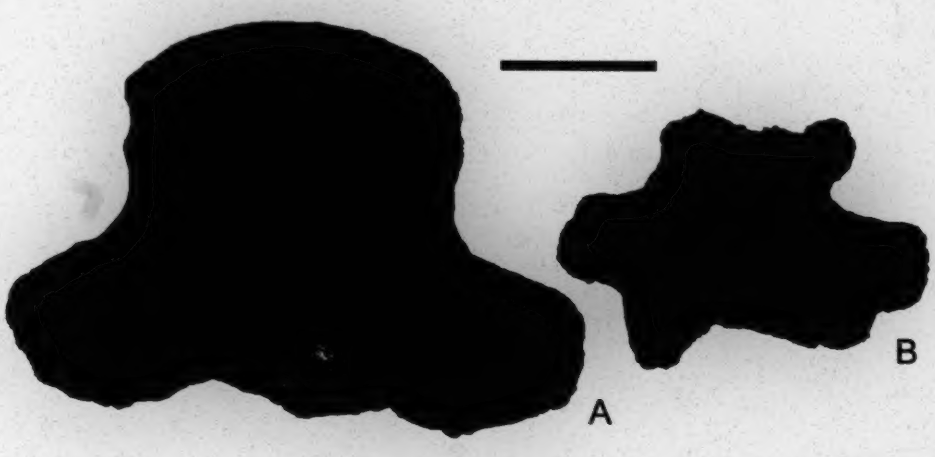


FIGURE 2-5. Comparison of dorsal vertebrae preserved in the type of *Tylosaurus pembinensis*, MT 2. **A**, a typical dorsal vertebra. **B**, a smaller dorsal vertebrae articulated within the caudal series. Note the difference in overall vertebral size and development of zygopophyses. Scale bar equals 50 mm.



Chapter 2. The youngest species of *Tylosaurus* (Reptilia: Squamata) from the Late Campanian Bearpaw Formation of Saskatchewan

Prepared for the Journal of Vertebrate Palaeontology.

THE YOUNGEST SPECIES OF *TYLOSAURUS* (REPTILIA: SQUAMATA) FROM THE LATE CAMPANIAN BEARPAW FORMATION OF SASKATCHEWAN

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RH: BULLARD—YOUNGEST SPECIES OF *TYLOSAURUS*

ABSTRACT—The tylosaurine mosasaur *Tylosaurus saskatchewanensis*, sp. nov., is described from the Late Campanian Bearpaw Formation of Saskatchewan. This new species exhibits several features not previously observed in tylosaurines, including the exclusion of the prefrontal from the dorsal rim of the orbit by the postorbitofrontal, and paired extensions of the frontal that underlie the premaxilla well into the external naris. Though it possesses considerably more vertebrae anterior to the chevron-bearing caudals than is typical of *Tylosaurus*, an assignment to *Hainosaurus* was deemed untimely given the current confusion surrounding this genus. This species extends the stratigraphic range of *Tylosaurus* into the Late Campanian.

INTRODUCTION

The mosasaur genus *Tylosaurus* has had a long and complicated history. It was the first mosasaur described from Kansas, when Cope (1869) assigned a fragmentary skull from the Niobrara Chalk to *Macrosaurus* Owen, naming it *Macrosaurus proriger*. One year later he referred the species to *Liodon* Owen (Cope, 1869-1870). Marsh (1872a) had at his disposal a good skeleton of this new mosasaur, as well as several other fragmentary specimens, and proposed a new genus *Rhinosaurus*, which was preoccupied by a lizard, to include all of Cope's species. Cope (1872) maintained that *Rhinosaurus* was the same as *Liodon*, but advanced the name *Rhamphosaurus*, also preoccupied by a lizard, should they prove to be different. Marsh (1872b) called attention to the preoccupation of Cope's name, and proposed the name *Tylosaurus* in its stead.

Tylosaurus is now one of the best understood of all mosasaur genera, thanks to some exceptionally complete specimens (Osborn, 1899) and enormous collections from the Niobrara Chalk. Two species of *Tylosaurus* were recognised by Russell (1967), *T. proriger* and *T. nepaeolicus*, but three other species represented by fragmentary material have been described: *T. capensis* (Broom, 1912), *T. imbeensis* (Lingham-Soliar, 1992), and *T. ivoensis* (Lindgren and Siverson, 2002). *Tylosaurus* is united with other genera into the subfamily Tylosaurinae on the basis of a toothless premaxillary rostrum. Other tylosaurines include *Taniwhasaurus* (Caldwell et al., 2005), *Hainosaurus* (Lingham-Soliar, 1992), and *Lakumasaurus* (Novas et al., 2002).

Here I describe a new specimen of tylosaurine mosasaur, RSM P 2588.1. This new specimen was collected in 1995 from the Bearpaw Formation near Herbert Ferry on the shore of Lake Diefenbaker, an artificial reservoir of the South Saskatchewan River. Upon collection and preparation, P 2588.1 was provisionally identified as *Hainosaurus* because of its young age and obvious tylosaurine affinities. To understand this new specimen better, I researched the literature on *Hainosaurus* and examined the only North American material of *Hainosaurus*, Nicholls' (1988) *H. pembinensis* from the Middle Campanian Pierre Shale of Manitoba (Chapter 2). I found that the anatomy of *H. pembinensis* was in need of clarification, as were some important characteristics of *H. bernardi*. Many anatomical details used by previous authors to separate *Hainosaurus* from *Tylosaurus* were found to be incorrect, or at best ambiguous. Indeed, there is no justification for a generic assignment to *Hainosaurus* based on the Manitoba material, and Lingham-Soliar's (1992) review of *H. bernardi* has not provided a satisfactory alternative (Chapter 2). Given the great similarity of Nicholls' Manitoba material to *Tylosaurus*, and the lack of a competing definition of *Hainosaurus*, I assigned her species to *Tylosaurus*. This same approach has been followed here for the new species.

Institutional abbreviation—RSM, Royal Saskatchewan Museum, Regina, Saskatchewan.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Linnaeus, 1758

Order SQUAMATA Oppel, 1811

Family MOSASAURIDAE Gervais, 1852

Subfamily TYLOSAURINAE Williston, 1897

Genus *TYLOSAURUS* Marsh, 1872b

Type Species—*Tylosaurus proriger* (Cope, 1869).

Range—Late Coniacian to Late Campanian.

Generic Diagnosis—See Russell (1967:171–173).

TYLOSAURUS SASKATCHEWANENSIS, sp. nov.

(Figs. 3-1–3-5)

Etymology—After Saskatchewan, the province in which it was collected.

Specific Diagnosis—Exclusion of prefrontal from dorsal margin of orbit by the postorbitofrontal; internarial bar of premaxilla embraced by paired processes of frontal that extend half length of external naris; on quadrate, suprastapedial process of moderate size, infrastapedial process low and rounded; femur longer than humerus; 52 vertebrae anterior to chevron-bearing caudals.

Holotype—RSM P 2588.1, a nearly complete skull, vertebral column missing much of the tail and disarticulated appendicular skeleton lacking most of the metapodials and phalanges.

Locality and Horizon—Collected near Herbert Ferry, Saskatchewan, on the shore of Lake Diefenbaker, an artificial reservoir of the South Saskatchewan River. In this valley, the Bearpaw is present as a series of alternating dark grey silty mudstones and brownish sandstones, with bentonite layers and calcareous concretions locally abundant (Caldwell, 1968). Ammonite fossils are known from the area (Riccardi, 1983), and specimens of *Plioplatecarpus* sp. and a *Mosasaurus* resembling *M. conodon* have been collected (Russell, 1993; pers. obs.). In terms of the ammonite biostratigraphy of the Western Interior, the Bearpaw Formation extends from about the Zone of *Didymoceras stevensoni* to the Zone of *Baculites grandis* (Caldwell, 1968), from the early Late Campanian to the Early Maastrichtian (Kauffman et al., 1993). Caldwell (1968) recognised eleven members of the Bearpaw along the South Saskatchewan River valley; P 2588.1 was collected from the Snakebite Member, which includes the Zones of *Baculites cuneatus* through *Baculites jenseni* (North and Caldwell, 1970; Caldwell et al., 1993), and so has a latest Late Campanian age (Kauffman et al., 1993).

DESCRIPTION

Cranium

The skull of P 2588.1 was preserved with its left side lying upwards, but the left side was displaced dorsally relative to the right, so that the jaws and palate were visible on the original upper surface. The left and medial portions of the suspensorium were badly damaged due to the torsion of the skull. After collection, the skull jacket was flipped and prepared on the right. This exposed the complete right side of the skull, as well as the skull roof (Fig. 3-1).

Premaxilla—A toothless rostrum projects 76 mm in front of the first premaxillary teeth, cylindrical in cross section and rectangular in lateral profile (Fig. 3-1). A small, laterally elongate tubercle is present on the under surface of the rostrum, 24 mm in front of the first teeth. The lateral and dorsal surfaces of the premaxilla are pierced by large, anterior-facing foramina, extending in a paired row back to about the level of the maxillary contact. The premaxilla diverges medially from the maxilla to form the internarial bar 325 mm behind the tip of the rostrum, above the anterior edge of the 4th maxillary tooth, and extends about the same distance again to an extensively interdigitating suture with the frontal (Fig. 3-2). At its forward origin the internarial bar is roughly rectangular in cross section, with pinched lateral margins. The bar quickly tapers to become cylindrical and parallel-sided behind, bearing on its lateral margins a shallow groove. At its posterior end the internarial bar is divided in two by a median process from the frontal, and developed into a pair of elongate processes that embrace this process laterally and extend well onto the main portion of the frontal (Fig. 3-2B). The frontal's median process occupies a shallow groove in the internarial bar anteriorly, but this groove gradually deepens until the premaxilla is completely bifurcated. The paired processes of the premaxilla gradually thin from this point to terminate as mere splints on the lateral faces of the frontal's median keel.

A pair of teeth is present on each ramus, bearing a single anterior carina. The anterior carina is place lingually and curves further lingually as the tooth develops. The tips of the teeth are asymmetrical in cross section, the carinate anterior margin is acuminate while the posterior margin is rounded.

Maxilla—The maxilla is a long, robust bone, extending 637 mm from the premaxillary suture to its termination behind the jugal. A row of anterior-facing foramina extend along most of the bone's length, 3–4 cm above the tooth row. The anteriormost point of suture with the premaxilla is in the form of a "double buttress" (sensu Lingham-Soliar, 1992), two short and rounded tongues of the maxilla extending toward the premaxilla (Fig. 3-1). Behind this "double buttress" the suture extends in a gently curved line backward to the tip of the external nares. The nares begin about 17 cm back from tip of the maxilla, above the anterior edge of the 4th maxillary tooth, and finish about 46 cm back, above the anterior edge of the 10th maxillary tooth (Fig. 3-1). Behind the premaxillary suture the dorsal margin of the maxilla is scalloped by a shallow, rounded embayment.

The area of anterior contact with the prefrontal is badly crushed, but the suture between these elements appears to be roughly triangular. Above the damaged area it is clear that the maxilla forms the entire lateral border of the external nares. At its posterodorsal end the maxilla terminates in a slender process that extends behind the external nares about 4 cm, to occupy a corresponding groove in the prefrontal. Ventrally, the maxilla contacts the jugal on the anteroventral corner of the orbit (550 mm behind the double-buttressed suture with the premaxilla). An elongate process of the maxilla extends along the medial side of the anterior jugal as far as the middle of the orbit.

Twelve teeth are present in the maxilla (Fig. 3-1). The teeth are robust and gently recurved. Tooth crowns bear two faintly serrated carinae, the lingual surface is inflated relative to the buccal. The tips of the crowns are ovoid in cross-section, but become more circular as the tooth develops. The enamel at the base of fully erupted crowns is subtly facetted, and bears faint vertical striations. Fully erupted teeth have a large bony base fused to the alveolar margin, and a slightly raised rim marks this union. The marginal dentition is unusually large and tightly spaced: fully erupted maxillary teeth are so long that they fit into corresponding pits in the margin of the dentary.

Frontal—This is the large, triangular element typical of mosasaurs (Fig. 3-1). A tall median keel is present on the anterior half of the frontal. It is continuous with a thin process that extends well forward to overlap the dorsal midline of the internarial bar of the premaxilla, occupying a gradually deepening groove in this element (Fig. 3-2B). The internarial bar bifurcates about this median extension of the frontal, extending onto the lateral faces of the keel as thin splints of bone. The posterior end of the internarial bar is also embraced laterally by broad paired projections of the frontal that extend forward 152 mm, over half the length of the external nares (Fig. 3-1). Behind these anterior processes, the margin of the frontal curves backward to meet the maxilla, this contact forms the posterior termination of the external nares. The frontal extends backward from the maxillary contact in a nearly straight line, barely emarginate over the orbits, to its posterior angulation above the postorbitofrontal. The posterolateral margin is scalloped by the postorbitofrontal. The posterior margin was damaged by the disruption of the parietal, but the frontal-parietal suture must have been nearly straight and the parietal foramen located at or very near the suture.

Prefrontal—The prefrontal is crushed along its anterior contact with the maxilla, but the suture between these two bone appears to be triangular (Fig. 3-1). It is completely excluded from the posterolateral margin of the external nares by the maxilla and from the dorsal rim of the orbit by the postorbitofrontal. The prefrontal bears a narrow groove on its anterodorsal margin which receives a posterior process from the maxilla. Above the orbit the prefrontal is heavily excavated on its lateral face, receiving a rounded anterior process of the postorbitofrontal. The lacrymal is present along its ventral suture with the maxilla.

Lacrymal—The lacrymal is a small triangular bone forming some of the anterior margin of the orbit, lying between the prefrontal and the maxilla (Fig. 3-1). Dorsally it overlaps the prefrontal, while ventrally it is in turn overlapped by the maxilla. There is no evidence of the lacrymal foramen typical of this element in other squamates.

Sclerotic Ring—A series of sclerotised plates are present in the right orbit (Fig. 3-1). The external margin of this ring is 125 mm wide anteroposteriorly, and about 100 mm deep dorsoventrally. The internal margin of the ring is 42 mm by 13 mm. There are at least eight separate plates present. Each plate is gently convex, and has a finely striate outer surface.

Postorbitofrontal—This is a complex, quadriradiate bone (Fig. 3-1). The anterior process is very extensive, overlapping the prefrontal to form the entire dorsal margin of the orbit. The ventral process extends down about half the height of the orbit, overlapping the jugal with a rounded process. The posterior process overlaps a similar process from the squamosal for much of its length, gradually pinching out posteriorly. The medial process is short and curved, articulating loosely with the parietal.

Jugal—The jugal is an L-shaped bone (Fig. 3-1). The dorsal process is laterally compressed. The anterior process is teardrop-shaped in cross section, the pinched edge pointing laterally, with a convex dorsal surface and a concave ventral surface. The posteroventral angle is obtuse, about 110 degrees. The posteroventral corner bears a striated tuberosity.

Parietal—The parietal was badly distorted by the torsion of the skull (Fig. 3-1). Its dorsal surface is nearly intact, but the ventral surface is badly crushed. The contact between the frontal and the parietal is damaged, but the parietal foramen is evidently located at or very near the frontal suture and is in the shape of a longitudinally elongate oval. The main body of the parietal tapers gradually behind the frontal-parietal contact, reaching its narrowest point slightly in front of the diverging suspensorial rami. The parietal table is uniformly flat. At its posterior end, between the suspensorial rami, the bone surface is grooved, probably representing the insertion of the M. spinalis capitis and M. rectus capitis posterior (Russell, 1967:28). There was evidently a broad area of insertion for the cervical musculature as in *T. proriger* (Russell, 1967:fig. 93).

The suspensorial rami are dorsoventrally flattened and diverge from the parietal table at about 45 degrees to the perpendicular. A thin process from the supratemporal underlies each ramus ventrally; the medial termination of this process is sandwiched by a thin ventral sheet of the parietal.

Quadrate—The right quadrate is the better preserved of the two, but because it remains in articulation with the skull, it is only visible in lateral aspect (Fig. 3-1). The left quadrate was removed from the matrix during preparation, and so allows examination of the anterior, posterior and medial surfaces, but it has been crushed dorsoventrally and anteroposteriorly (Fig. 3-3). The following reconstruction of the quadrate is based largely on the left quadrate, corrected for the distortion in this element, and supplemented where possible by the right.

The quadrate shaft is straight and anteroposteriorly compressed (Fig. 3-3C). It is narrow dorsally, but expands ventrally into the transversely broad ventral condyle. The medial corner of the dorsal shaft is square in anteroposterior view, from there the bone extends ventrolaterally in a gentle arch, forming a convex dorsal condyle for articulation with the suspensorial arcade of the skull. A polished but irregular condylar surface covers the narrow dorsal surface and continues downward onto the top of the alar crest and the suprastapedial process. The alar crest is present about one third of the way down the dorsal surface, extending anterolaterally from the shaft. The suprastapedial process is developed from the posterior face of the shaft. Unfortunately, in both quadrates the suprastapedial is poorly preserved, in the right it is obscured and the left is broken at the base (Fig. 3-3D). This broken base on the left element indicates that the suprastapedial was of moderate size, at least at its origin, though its total extent remains undetermined.

The medial face of the shaft, like the lateral, is not extensive (Fig. 3-3C). A narrowly rounded ridge extends from the medial corner of the dorsal condyle to the same corner of the ventral condyle, this is the "median ridge" of Bell (1997:311). This ridge is straight in medial view (Fig. 3-3C). The stapedial pit is in the shape of a rounded rectangle. It is 18 mm in longest dimension and 6 mm wide, and its long axis is oriented obliquely posterolaterally.

The anterior face of the quadrate is poorly preserved in the left quadrate (Fig. 3-3B), and obscured in the right. The anterior shaft is narrow dorsally and broad ventrally, but most of the surface is dominated by a large tympanic ala. From the tip of the alar crest dorsally, a very thin (about 1–2 mm) tympanic ala is developed anteriorly from the shaft. This ala is highly concave, being nearly as broad mediolaterally as the quadrate shaft is in this dimension. The tympanic rim, following the lateral edge of the ala, is sharp and thin, and has a hemispherical outline in lateral view (Fig. 3-1). The rim curves sharply at the ventrolateral corner of the bone, and continues dorsoposteriorly in a straight line, terminating on the lateral face of the infrastapedial process, forming the "posteroventral ascending tympanic rim" (sensu Bell, 1997).

The posterior face of the shaft is restricted dorsally, but extensive ventrally (Fig. 3-3D). The dorsal half of the shaft is dominated by the suprastapedial process. From the median ridge, the dorsal condyle curves gently, following the suprastapedial process in its medial flexion. The meatal notch is present near middle height. A rounded sulcus extends from the medial origin of the infrastapedial process, around the medial side of the stapedial pit, to disappear slightly above the pit. At the top of the lower third of the shaft, the infrastapedial process is moderately developed. In mediolateral view, the process slopes uniformly to a rounded tip (Fig. 3-3A). The medial face of the process is precipitous, due to the proximity of the sulcus, but it recedes gently into the notch dorsally and the posterior shaft ventrally.

The ventral condyle is a polished but irregular surface covering the ventral surface of the shaft. In ventral view, the condylar surface is in the shape of a mediolaterally elongate oval. The only deviation from this shape is a short triangular extension of the surface dorsally onto the anterior face of the shaft, at the midline of the bone (Fig. 3-3B). The outline of the ventral condyle is convex in mediolateral view, in anteroposterior view it is slightly concave towards the medial edge.

Dentary—The dentary is a gently curved and uniformly tapered bone. Its anterior tip is semirectangular in outline and edentulous for 47 mm in front of the first tooth. The posterior border is irregular and heavily textured by longitudinal grooves; it bears a large sulcus, for reception of the M. angulari oris as in *Varanus*, on its posterodorsal margin. Anteroposteriorly elongate foramina pierce the bone below the alveolar margin.

There are thirteen teeth, all fully erupted and bearing a raised rim around the bony base. The dental morphology is very similar to that of the maxilla: teeth are robust and gently recurved. There are two carinae and the lingual face is inflated.

Splenial—The articular surface for the angular is semicircular in shape, slightly concave, and sloped very slightly to the posterior.

Angular—The articular surface for the splenial is semicircular and slightly convex, sloping slightly to the posterior.

Surangular—The surangular is a triangular bone, forming much of the lateral face of the posterior jaw (Fig. 3-1). The anterior margin, bordering the intramandibular joint, is irregular and heavily striated. The anterodorsal edge of the surangular receives the coronoid along a curved suture. The dorsal margin extends in a straight line back to its contact with the articular, where the surangular is excavated to form the anterior and lateral surfaces of the glenoid. These surfaces represent about one quarter of the total area of the glenoid fossa, and face posterodorsally and medially. From the posterolateral corner of the glenoid fossa, the posterior margin of the surangular curves sharply around to the anterior, and then follows a gentle curve to the anteroventral corner of the bone.

Coronoid—Much of this crescentic bone is concealed beneath the jugal. Its dorsal portion has a straight posterior margin. The anterior portion projects 88 mm in front of the surangular, extending above the intramandibular joint. The ventral contact with the surangular is a gentle curve, convex ventrally, which slopes towards the anterior.

Articular—The anterodorsal surface of the articular forms the larger posterior portion of the glenoid fossa, a smooth semicircular surface which faces anterodorsally and medially. Behind the glenoid the articular curves medially and ventrally, forming the retroarticular process. In lateral view, the retroarticular process has a rounded dorsal margin, and a straight ventral margin that is oriented obliquely ventrally (Fig. 3-1).

Appendicular Skeleton

Scapula—The scapula is a robust hemispherical bone, though only half the area of the coracoid (Fig. 3-4A). It measures 99 mm between the glenoid articular surface and the dorsal margin. The ventral edge bears a pair of roughened oval articulations, a posterior glenoid facet and a ventromedial coracoid facet, separated from each other by a slight mediolateral constriction. The coracoid facet is continuous with a roughened and unfinished margin along the anterior and superior borders, representing the point of attachment of a large cartilaginous suprascapula (Osborn, 1899). From the anterior tip of the coracoid facet, this rough margin arcs backward about 180 degrees about the center of the bone, terminating above the glenoid facet. The bone's circumference is finished by a smooth, flexed posterior margin that lies nearly vertical above the glenoid facet. The medial face of the bone is slightly concave in both planes, the lateral face slightly convex vertically. Radial striations cover the lateral and medial faces of the bone's margins.

Coracoid—The coracoid is broadly expanded, considerably larger than the scapula (Fig. 3-4A). It measures 171 mm between the glenoid articular surface and the midpoint of the medial margin. The dorsal head of the bone bears a pair of roughened articulations: a semicircular glenoid facet facing dorsolaterally, merging anteriorly into a lower, triangular scapular facet. Below the head the coracoid constricts slightly, this neck is pierced anteriorly by a circular foramen marking the passage of the nerve for the M. supracoracoideus (Russell, 1976). Medially the bone continues to flatten dorsoventrally, the anterior edge remaining thicker than the posterior, but expands again into a transversely elongate fan. The anterior margin of this fan is weakly concave and barely longer than the curved posterior margin. The medial border is strongly arched and irregularly roughened, with a slight notch as in some specimens of *Tylosaurus* (Osborn, 1899:fig. 9).

Humerus—The humerus is an elongate bone, though only 172 mm in length, with well-developed processes (Fig. 3-5A). The condyles are heavily pitted and roughened and would have been capped by thick cartilages in life. The proximal end of the bone is expanded anteroposteriorly, to nearly the same width as the distal end, and bears a triangular articular surface formed from the deltoid tuberosity anteriorly, the postglenoid process posteriorly, and the pectoral crest anteroventrally. The glenoid condyle and postglenoid process are not clearly separated on this surface, but the postglenoid process is deflected distally. The pectoral crest is robust and distinctly developed from the ventral face of the shaft. The deltoid tuberosity is extended distally, forming a prominent process on the anterior face of the shaft. The humerus constricts towards the midlength of the bone, but expands again anteroposteriorly to form strongly arched anterior and posterior margins in dorsal view. The distal end of the bone bears a single, continuous articular surface formed from an anterior radial facet and a posterior ulnar facet separated by a slight constriction, with a small ectepicondyle and large, thin entepicondyle present as proximal flexions. Above the radial facet on the dorsal surface, the ectepicondylar foramen is present as a lengthy penetration of the bone.

Radius—This is an elongate element, 135 mm in length, though broader than the ulna (Fig. 3-5A). The proximal and distal ends bear an oval articular facet, the surface of which is slightly concave and irregularly roughened. Distally the shaft constricts to the midpoint of the bone. The posterior border of the bone expands again, but the anterior edge is drawn out into a curved flange. The outer surface of this flange is irregularly roughened, and merges with the distal articular surface of the shaft.

Ulna—This is an elongate element, 124 mm in length, with the ends barely expanded (Fig. 3-5A). The proximal head bears a flat, semitriangular articular surface. A small, barely distinct olecranon process is developed on the posterior face of the shaft, its articular surface continuous with that on the proximal surface of the bone. The bone shaft constricts slightly at its midpoint, though the distal end of the bone is no more expanded than the proximal. The distal articular surface is lenticular, and deflected proximally towards the posterior margin of the bone.

Illium—The ilium measures 298 mm from the ventral margin to its dorsal termination (Fig. 3-4B). The ventral head is expanded into an anteroposteriorly oval articulation, which faces ventrolaterally into the acetabulum. The surface of this articulation is convex and slightly roughened. Above the head, the shaft narrows, becoming mediolaterally compressed, and curves gently anteriorly before straightening for the remainder of its length. The dorsal tip is simply rounded.

Ischium—The ischium measures 159 mm in maximum length (Fig. 3-4B). The dorsal articular surface is roughly triangular, with one apex of the triangle pointing medially; the surface of this articulation is roughened. Below the dorsal head the shaft constricts laterally. A low, rounded crest extends from the posterodorsal to the anteroventral corners of the bone on the lateral side. The ischiadic tubercle is developed as a long, thin, triangular projection slightly above middle height on the posterior edge of the shaft. The ventral tip is abruptly squared off.

Pubis—The pubis measures 209 mm in maximum length (Fig. 3-4B). The dorsal articular surface is broadly oval in shape, gently convex and irregularly roughened. Anteriorly it merges with a small, oval articular surface at the head of the pubic process. The pubic process is present only as a narrow ridge of bone on the anterior face of the bone. Just ventral from the head, towards the anterior edge of the bone, is the obturator foramen, an oval penetration. Below the dorsal head the pubis constricts; the shaft becomes laterally compressed, its posterior margin narrower than the anterior, with a concave medial surface. Ventrally the bone ends abruptly as a straight, but slanted surface.

Femur—The femur is a large and well-developed bone, 182 mm in length (Fig. 3-5B). The proximal head is roughly circular, merged with a large, rounded internal trochanter on the anteroventral face of the shaft; the surface of both is heavily roughened. The shaft of the femur is constricted at its midpoint, distally it expands anteroposteriorly. The distal articular surface takes the form of an anteroposteriorly elongate oval, convexly arched. The tibial and fibular facets are merged into a single roughened surface, though the anterior tibial facet is slightly thickened dorsoventrally (57 mm vs. 42 mm) and faces laterally, while the posterior fibular facet faces posterolaterally.

Tibia—The tibia is only 117 mm in length, but considerably broader than the fibula (Fig. 3-5B). The proximal articular surface is an anteroposteriorly elongate oval, slightly concave and irregularly roughened. The shaft is constricted, slightly dorsoventrally but strongly anteroposteriorly, giving it an hourglass profile. The posterior margin of the shaft, bordering the crural foramen, is broadly rounded, while the anterior margin thins uniformly into an elongate flange on the distal end of the shaft. This anterior flange has a roughened margin which merges seamlessly into the distal articular surface. The distal articular surface is roughly diamond-shaped. Its irregular surface is strongly arched anteroposteriorly, with a strong posterior flexion for the astragalar facet.

Fibula—This is an elongate bone, 112 mm in length, only slightly expanded at both ends (Fig. 3-5B). The proximal articular surface is oval and irregularly roughened. The shaft of the fibula constricts at the midpoint, and become slightly flexed posteriorly. Its cross section is roughly oval, with the anterior edge slightly thicker. The distal end is fan-shaped, its articular surface an anteroposteriorly elongate oval.

Astragalus—This is a semicircular disc of bone, 51 mm in diameter, thickened slightly towards the margins (Fig. 3-5B). Its margin is rough and unfinished, save for a semicircular notch bordering the crural foramen.

Metacarpals and Phalanges—Both metacarpals and phalanges are elongate, cylindrical elements, slightly expanded at both ends, with abrupt, unfinished tips (Fig.

3-5). There is little difference between the manus and the pes, though the elements of the pes are stouter. Phalanges of the fifth digit are relatively shorter, flatter, and more expanded than those of the other digits.

Vertebral Column

Cervical Vertebrae—All the elements of the atlas and axis are present but slightly dissociated. The synapophysis of the atlas neural arch is present as a tubercle on the posterior margin. The spinous process is short, less than two-thirds of the height of the main body of the neural arch, and would not have contacted the opposite process. The posterior condyle of the axis centrum is circular in shape. The condylar surfaces and centrum of the third cervical are also circular, but more posterior vertebrae become increasingly depressed and ovoid in form. Zygopophyses are well developed on all the cervicals, but zygosphenes and zygantra are entirely absent. Synapophyses are located ventrally on the midpoint of each centrum. Hypapophyses are not fused, articulating with a subcircular depression on the posteroventral margin of the cervical centra. The hypapophysis itself is posteriorly recurved, and slightly laterally compressed.

If cervical vertebrae are defined as those preceding the first vertebra with a rib connecting to the sternum (Romer, 1956), the number of cervicals cannot be counted without a complete series of ribs in articulation. In P 2588.1, only the first six vertebrae (counting the atlas and axis) bear articulated hypapophyses, while four vertebrae posterior to these have raised protuberances in the same position. The sixth cervical is also the last hypapophysis-bearing vertebra in *Platecarpus* and *Tylosaurus* (Russell, 1976:76), and it is perhaps reasonable to conclude that there are seven cervical vertebrae in P 2588.1 as there are in the former species (Osborn, 1899; Williston, 1910).

Dorsal Vertebrae—If we assume that there are 7 cervicals, 36 dorsal vertebrae are preserved in P 2588.1. The shape of the first dorsal centrum is a slightly depressed ovoid like the final cervical, but more posterior vertebrae become increasingly dorsoventrally flattened, quickly taking on an oval form. This oval form is gradually elongated vertically, so that by the twentieth dorsal the centra have become triangular in cross section, with one apex of the triangle pointing dorsally. Zygopophyses are reduced in size posterior in the dorsal series, becoming obsolete after the eighteenth dorsal vertebra. Synapophyses are located at the anterodorsal edge of the centrum. Neural spines are incompletely preserved, but are generally very thin. Neural spines of anterior dorsals are inclined to the posterior, while spines of posterior dorsals are more vertical in orientation. It is impossible to divide the dorsal series into thoracic and lumbar regions because these regions are defined by the length of their ribs (Russell, 1967:76–77), and no ribs are preserved in articulation.

Ribs—Several ribs are preserved in P 2588.1; though located roughly in the thoracic cavity, none of them are in articulation with their vertebrae. They are long and moderately arched, with slightly expanded and flattened extremities.

Caudal Vertebrae—Only 9 pygal vertebrae are preserved. The centra and condylar surfaces are triangular, identical in form to posterior dorsals. Synapophyses are long, thin, and gently tapered. At least thirty caudals are present posterior to the pygals, but most of these disarticulated and heavily weathered. Chevrons are unfused. Preserved in articulation with the pygals there are 7 caudals with both chevrons and transverse processes. Fragments of at least 23 more caudals can be identified, of varied diameters, most of them probably terminal caudals.

DISCUSSION

With the older species of *Tylosaurus*, *T. saskatchewanensis* shares the pronounced, toothless rostrum typical of tylosaurines, exclusion of the prefrontal from the narial margin by the maxilla, and moderately-sized suprastapedial and infrastapedial processes. It most closely resembles *T. proriger* and *T. pembinensis*: the premaxillary rostrum is rectangular in lateral profile, the external nares begin above the fourth maxillary tooth, the parietal foramen is close to the frontal suture, the postorbitofrontal overlaps the prefrontal above the orbit, and the cervical epaxial musculature has an extensive insertion on the posterior parietal. The postorbitofrontal's overlap of the prefrontal is more extensive than in both these species, however, reaching the anterodorsal corner of the orbit and completely excluding the prefrontal from dorsal orbital margin (Fig. 3-1–3-2). The appendicular skeleton resembles that of *T. pembinensis* in the greater development of processes, compared to *T. proriger* (cf. Osborn, 1899; Russell, 1967:89–90), and the greater length of the femur compared to the humerus. The dental formula of 12 maxillary teeth and 13 dentary teeth is consistent with the known species of *Tylosaurus*, as well as *Hainosaurus*.

The quadrate of *H. bernardi* has a small suprastapedial process and an infrastapedial process that is reduced to a mere swelling (Lingham-Soliar, 1992:fig. 9). The tympanic cavity is shallow and confined, with a thin tympanic ala that is not strongly arched. This is very different from the condition in *Tylosaurus* (Russell, 1967:fig. 94), where the suprastapedial and infrastapedial processes are both of moderate size, and there is a strong, concave tympanic ala. The quadrate of P 2588.1 resembles that of *Tylosaurus* in the size of its suprastapedial and infrastapedial processes, and the development of the tympanic ala. It shares with *T. proriger* and *T. pembinensis* a posteroventral ascending tympanic rim that ascends high onto the lateral face of the infrastapedial process.

The vertebral formula of *T. saskatchewanensis* (Table 3-1) more closely matches that of *Hainosaurus* than *Tylosaurus*, having considerably more vertebrae anterior to the chevron-bearing caudals. Since this has been used as a method of diagnosing *Hainosaurus* (Russell, 1967; Nicholls, 1988), it would seem logical to assign P 2588.1 to that genus. In the other aspects of its anatomy, however, particularly the quadrate, P 2588.1 seems to resemble the species of *Tylosaurus*. In light of the uncertainties in our current understanding of *Hainosaurus* (Chapter 2), I have conservatively assigned it to *Tylosaurus*. Study of the type and referred material of *H. bernardi* may allow it to be reassigned.

The presence of a species of *Tylosaurus* in a fauna that can clearly be assigned to Russell's (1993) Navesinkian "age" makes *T. saskatchewanensis* the youngest known species of *Tylosaurus*. This gives the genus a very long temporal range for a mosasaur: from the Late Coniacian of the lower Niobrara chalk to the Late Campanian of the Bearpaw. The morphological similarity between known *Tylosaurus* species is remarkable given this lengthy geological span.

ACKNOWLEDGMENTS

The author is very grateful to Dr. Harold Bryant of the Royal Saskatchewan Museum, who made P 2588.1 available for study. The Natural Science and Engineering Research Council of Canada provided funding for much of this project.

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TABLE 3-1. Comparison of vertebral formulae in the tylosaurine mosasaurs discussed in this study. Data for *Tylosaurus pembinensis* from Chapter 2, for *T. proriger* and *T. nepaeolicus* from Russell (1967), and for *Hainosaurus bernardi* from Dollo (1887).

	T. saskatchewanensis	*T. pembinensis*	*T. proriger* and *T. nepaeolicus*	*H. bernardi*
Cervicals	7	7	7	10
Dorsals	36	29	22-23	19
Pygals	9		6-7	20
Precaudals[†]	52	36	36-37	49
Caudals[†]	>30	74	89-112	49
Total	>82	110	125-149	98

[†] 'Precaudals' are defined as those vertebrae anterior to the first chevron-bearing caudal, and 'caudals' as the vertebrae posterior to, and including, the first chevron-bearing caudal.

FIGURE 3-1. Skull of *Tylosaurus saskatchewanensis*, RSM P 2588.1, in right lateral view. **A**, edited photograph. **B**, labelled line diagram. **Abbreviations**: **a**, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **f**, frontal; **j**, jugal; **l**, lacrymal; **mx**, maxilla; **p**, parietal; **pmx**, premaxilla; **pof**, postorbitofrontal; **prf**, prefrontal; **q**, quadrate; **sa**, surangular; **sp**, splenial; **sq**, squamosal; **sr**, sclerotic ring. Scale bar equals 100 mm.

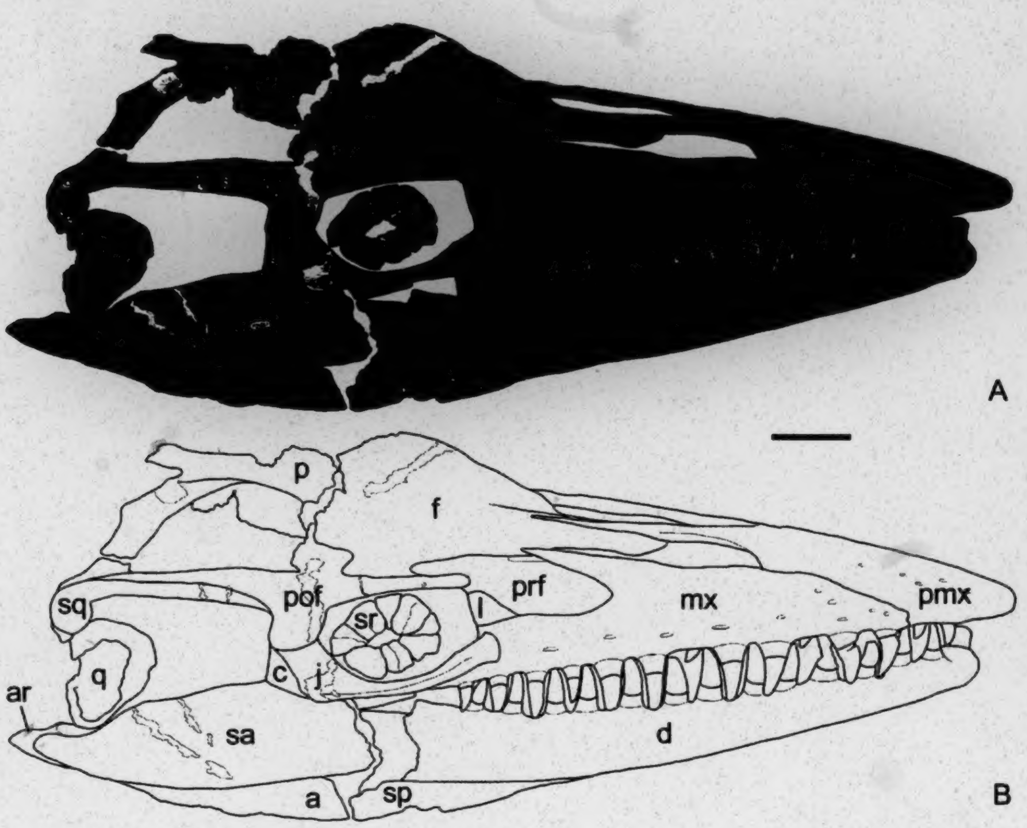
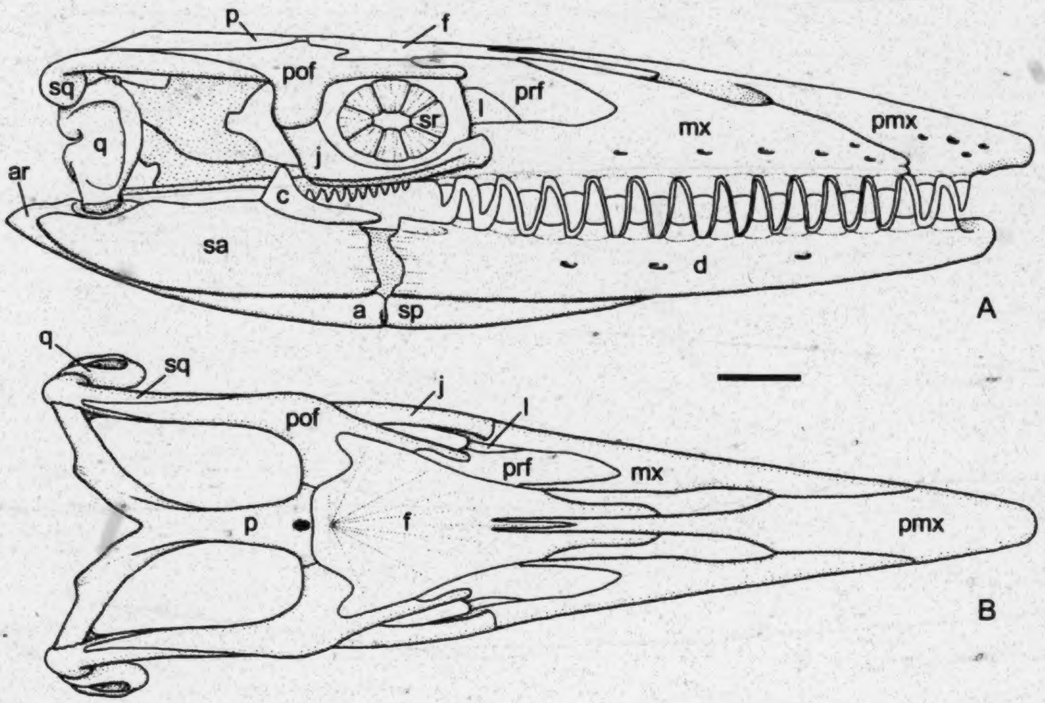


FIGURE 3-2. Reconstruction of the skull of *Tylosaurus saskatchewanensis*, after RSM P 2588.1. **A**, right lateral view. **B**, dorsal view. For abbreviations see Fig. 3-1. Scale bar equals 100 mm.


p
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j
pof
l
prf
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B

FIGURE 3-3. The left quadrate of RSM P 2588.1. **A**, lateral view. **B**, anterior view. **C**, medial view. **D**, posterior view. Scale bar equals 50 mm.

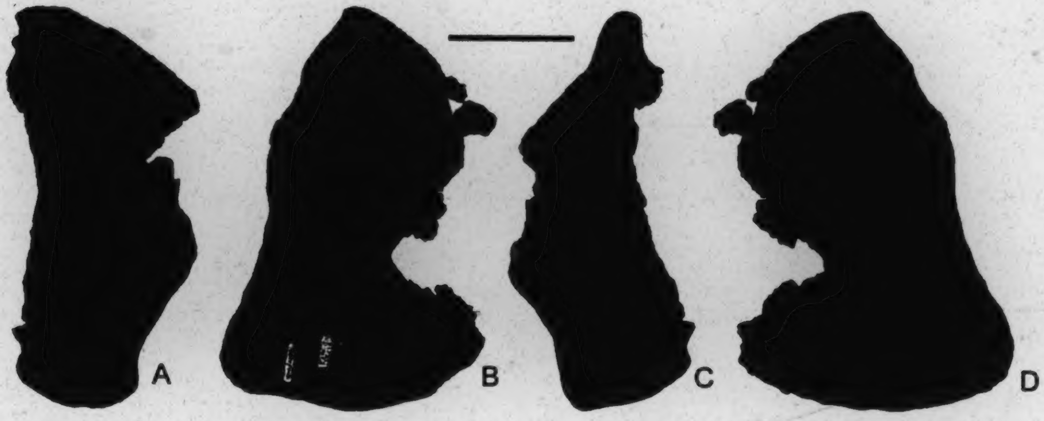


FIGURE 3-4. Pectoral and pelvic girdles of RSM P 2588.1 in lateral view. **A**, pectoral girdle. **B**, pelvic girdle. **Abbreviations**: **cor**, coracoid; **il**, ilium; **is**, ischium; **pub**, pubis; **sc**, scapula. Scale bar equals 50 mm.

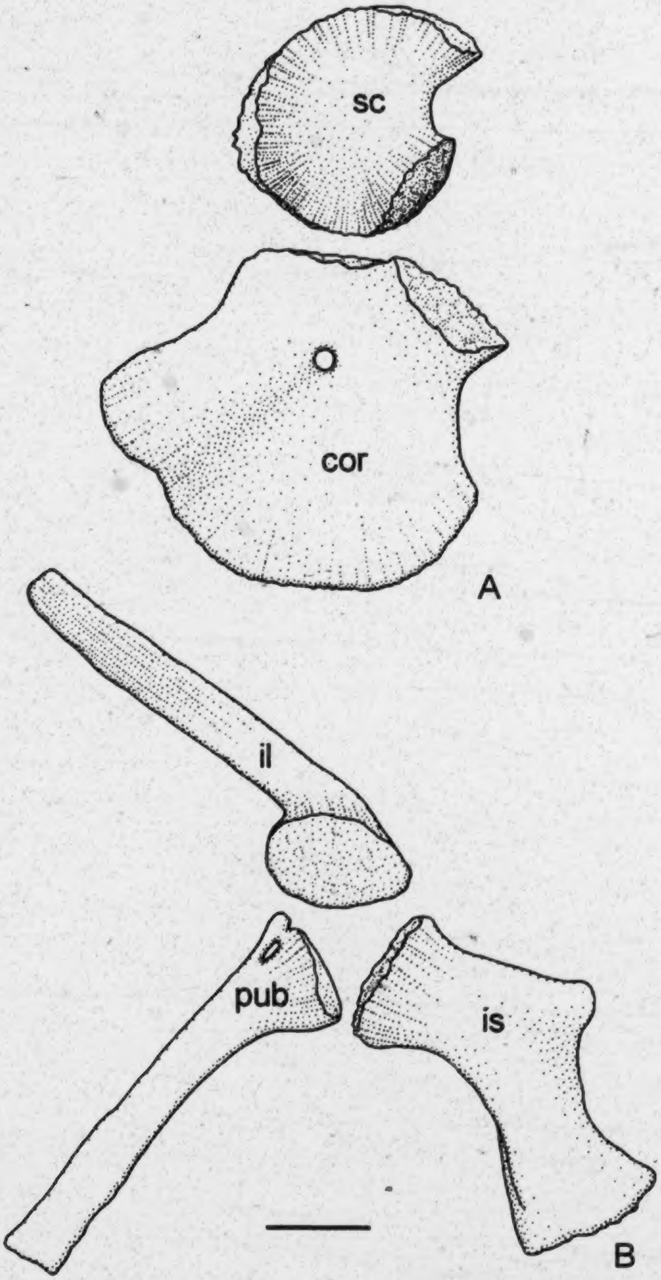
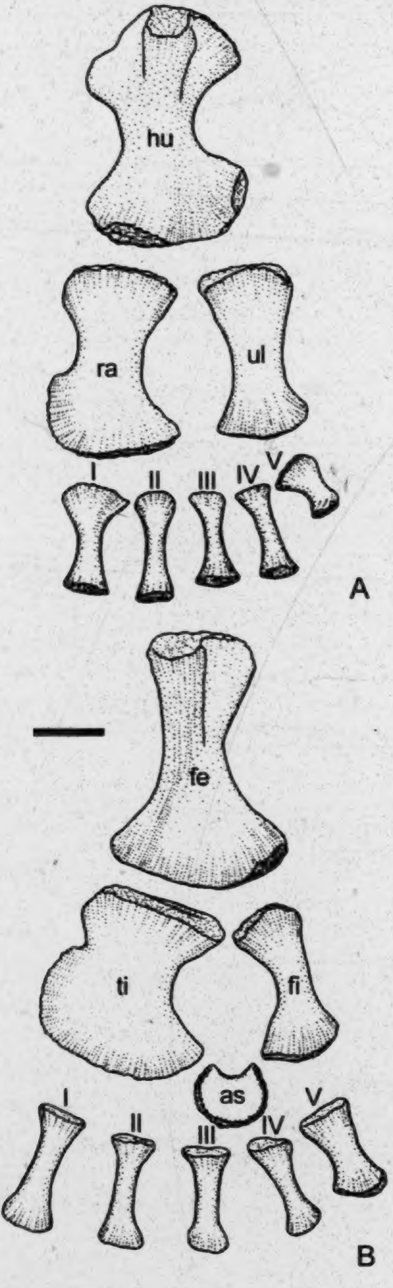


FIGURE 3-5. Proximal forelimb and hindlimb of RSM P 2588.1 in ventral view. **A,** forelimb. **B,** hindlimb. **Abbreviations**: **I–V**, metacarpals/metatarsals; **as**, astragalus, **fe**, femur; **fi**, fibula; **h**, humerus; **ra**, radius; **ti**, tibia; **ul**, ulna. Scale bar equals 50 mm.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Chapter 3. The phylogeny of tylosaurine mosasaurs (Reptilia: Squamata)

Prepared for the Journal of Vertebrate Palaeontology.

THE PHYLOGENY OF TYLOSAURINE MOSASAURS (REPTILIA: SQUAMATA)

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RH: BULLARD—PHYLOGENY TYLOSAURINE MOSASAURS

ABSTRACT—The phylogeny of the mosasaur Subfamily Tylosaurinae (Reptilia: Squamata) is the focus of a cladistic analysis of mosasauroids. Expanded descriptions of *Hainosaurus bernardi* and *Taniwhasaurus oweni* allow them to be included in a phylogenetic analysis for the first time. The results are consistent with those of previous workers, and show that there is strong support for the monophyly of the Tylosaurinae, but only weak support for the relationships among tylosaurine species. *Hainosaurus bernardi* and *Taniwhasaurus oweni* are the most primitive tylosaurines, with the species of *Tylosaurus* forming a monophyletic clade.

INTRODUCTION

The tylosaurines are a group of large mosasaurs characterised by an elongate, edentulous rostrum on the premaxilla. The first fossil possessing this distinctive anatomy was described by Cope (1869) as *Macrosaurus proriger*, but Marsh (1872) later referred it to the new genus *Tylosaurus*. Russell (1967) accepted two species from the Niobrara chalk of Kansas: *T. nepaeolicus* in the lower part of the chalk, and *T. proriger* in the upper part. Bell (1993, 1997) recognised a third species of *Tylosaurus* from Kansas in museum collections, but it was Everhart (2005) who formally described and named it *T. kansasensis*. Other, much less complete *Tylosaurus* species are known from other parts of the world, including *T. ivoensis* (Lindgren and Siverson, 2002) from Sweden, and *T. capensis* (Broom, 1912) from South Africa.

There are now three other genera of tylosaurine mosasaurs. The most complete of these is *Hainosaurus* (Dollo, 1885), represented by the type species, *H. bernardi*, from the Early Maastrichtian of Belgium, and two more species, *H. lonzeensis* (Dollo, 1904) and *H. gaudryi* (Bardet, 1990; Lingham-Soliar, 1992), that are much more fragmentary and of uncertain affinity. Hector (1874) described a pair of mosasaurs from the Late Cretaceous of New Zealand, *Taniwhasaurus oweni* and *Liodon haumuriensis*, but it was Welles and Gregg (1971) who recognised that both species were tylosaurines. Most recently, Caldwell et al. (2005) synonymised *Liodon haumuriensis* with *Taniwhasaurus*, and referred some new material. The newest genus of tylosaurine mosasaur, *Lakumasaurus*, has been described from Antarctica (Novas et al., 2002).

Many cladistic studies have examined the position of the Mosasauroidea within Squamata (eg. Rieppel, 1980; Carroll and deBraga, 1992; deBraga and Carroll, 1993; Caldwell, et al. 1995; Caldwell, 1999), with varied results, but comparatively few have been published on the interrelationships of mosasauroids and mosasaurs themselves (Bell, 1993, 1997; Caldwell, 1996). Bell's doctoral dissertation (Bell, 1993) was later revised (Bell, 1997), but the results of both analyses were very similar (Fig. 4-1). Most of the larger taxonomic groupings in Russell's (1967:fig. 99) phylogeny were maintained, though there were some differences at the generic level. In both Russell's (1967) and Bell's (1997) phylogenies, the tylosaurines are allied with the plioplatecarpines in a group Bell (1993) informally termed the 'Russellosaurines,' but later named the parafamily Russellosaurina (Polcyn and Bell, 2005). The studies of Bell (1993, 1997) and Caldwell (1996) have included *T. proriger*, *T. nepaeolicus*, and *T. kansasensis*, but the phylogenetic relationships within the Tylosaurinae have never been examined in further detail.

This study is an attempt to address some of the shortcoming of Bell's matrix with respect to the Tylosaurinae. The characters and states of Bell's (1997) matrix are reviewed, focussing on the three Kansas species of *Tylosaurus*. Improved descriptions of *H. bernardi* (Lingham-Soliar, 1992), *T. pembinensis* (Chapter 2), *Taniwhasaurus oweni* (Caldwell et al., 2005), and a new species of *Tylosaurus* (Chapter 3) allow them to be coded for Bell's (1997) characters, and included in a cladistic phylogenetic analysis for the first time. The large majority of Bell's (1997) data set has been retained without modification.

MATERIALS AND METHODS

The data set (Appendix 1) is modified from Bell (1997), containing 38 fossil taxa and an outgroup derived from living squamates. There are 136 unordered morphological characters (see Appendix 2). The data set was updated with the modifications to *A. buccichi* and *A. dalmaticus* recommended by Caldwell (1996:433); except where noted the characters and states (Appendix 2) are unchanged from Bell (1997).

Hainosaurus bernardi (after Lingham-Soliar, 1992), *Tylosaurus pembinensis* (Chapter 2), *T. saskatchewanensis* (Chapter 3), and *Taniwhasaurus oweni* (after Caldwell et al., 2005) were incorporated into Bell's (1997) data set. I was unable to secure a description of the new tylosaurine species *Lakumasaurus antarcticus* (Novas et al., 2002). To conserve computational time and reduce uncertainty in the resulting trees, the undescribed and most incomplete of Bell's (1997) taxa were excluded a priori: his "Taxon novum" (YPM 40383), and the Trieste and Dallas aigialosaurs.

Five of Bell's (1997) characters were excluded from the analysis. Character 9, the shape of the frontal, was sufficiently ambiguous that I could not reconcile it with published figures (Bell, 1997:fig. 6), nor code it for the added taxa. Character 12, the development of a dorsal keel on the frontal, was removed following Russell's (1967:20) and Bell's (1993:60) observation that the keel can be either absent or present in *Tylosaurus*, and Bell's (1993) suggestion that the character is highly plastic. Character 34, the extent of the postorbitofrontal along the lateral margin of the supratemporal fenestra, was also very ambiguous and difficult to reconcile with figures (Bell, 1997:fig.

6). Removal of the aigialosaur taxa made characters 15 and 124 of Bell's (1997) data set uninformative, and these were also removed.

The phylogenetic analysis was performed with PAUP* version 4.0 beta 10 (Swofford, 2003), using the heuristic search algorithm with the same settings used by Bell (1997): DELTRAN character optimisation, simple addition with one tree held at each step, TBR branch swapping, and steepest descent not in effect. All characters were left unordered, and the trees rooted on the outgroup taxon. To test branch support, bootstrap tests (Felsenstein, 1985) were performed on the data set using the same settings of the heuristic search as the phylogenetic analysis, over 100 replicates. Bremer support values were calculated by repeating the phylogenetic analysis and keeping all trees of progressively higher length.

RESULTS

The phylogenetic analysis resulted in 54 shortest trees of length 338, with a consistency index of 0.494 and a retention index of 0.804. The strict consensus tree (Fig. 4-2) and majority-rule consensus tree (Fig. 4-3) are very similar to each other and to Bell's preferred tree (Fig. 4-1), except that the strict consensus does not include a monophyletic Russellosaurina. The bootstrap tests give good support (80-100%) for Mosasauridae, Mosasaurinae, Plotosaurini, and Tylosaurinae, as well as clades containing the taxa of *Halisaurus*, *Plotosaurus*, and *Ectenosaurus*. Poor bootstrap support (50%-70%) is indicated for Natantia, Globidensini, and the Russellosaurina. Bremer support shows high values for the Mosasaurinae and Tylosaurinae, with moderate results for

Natantia, the sister-group position of *Halisaurus* to the Natantia, the taxon containing *Platecarpus* and *Plioplatecarpus*, and amongst the described species of *Tylosaurus*. These branch-support results are summarised in Fig. 4-3.

The nodes subtending the major clades of tylosaurine mosasaurs are labelled on Fig. 4-3. Node A, including the most recent common ancestor of the Tylosaurinae and all of its descendants, is diagnosed by 12 synapomorphies, three of which are unique, five are unequivocal, and two are equivocal. Node B, including the most recent common ancestor of *Taniwhasaurus oweni* and the species of *Tylosaurus* and all of its descendants, is supported by three synapomorphies. Node C, including the most recent common ancestor of the species of *Tylosaurus* and all of its descendants, is diagnosed by four synapomorphies, one of which is equivocal. Node D, including the most recent common ancestor of the species of *Tylosaurus*, except *T. kansasensis*, and all of its descendants, is supported by three synapomorphies. Node E, including the most recent common ancestor of *Tylosaurus proriger*, *T. pembinensis* and *T. saskatchewanensis* and all of its descendants, is diagnosed by three synapomorphies, one of which is equivocal. Node F, including the most recent common ancestor of *Tylosaurus pembinensis* and *T. saskatchewanensis* and all of its descendants, is supported by two synapomorphies. For a complete list of character transformations within the Tylosaurinae, see Table 4-1.

DISCUSSION

The results of this phylogenetic analysis agree very closely with those of Bell (1993, 1997), and there are no significant departures from his preferred tree (Fig. 4-1).

Bell (1997) also found the best support amongst the Mosasaurinae, and generally poor support within the Russellosaurina. The paraphyly of the Aigialosauridae is corroborated. The position of *Halisaurus* at the base of the mosasaurids is repeated, and the Globidensini remain part of the Mosasaurinae. The paraphyly of *Mosasaurus* and *Platecarpus* is maintained, though half of the shortest trees support the paraphyly of *Plesiotylosaurus* rather than *Prognathodon*. Support for Polcyn and Bell's (2005) Russellosaurina is weaker; the clade is resolved in only 2/3 of the shortest trees and has poor bootstrap support. This may be due to removal of Bell's (1997) ambiguous character 34, postorbitofrontal extent along the supratemporal fenestrae, which is listed as a russellosaurine synapomorphy.

Synapomorphies of the Tylosaurinae

The character transformations diagnosing the nodes within the Tylosaurinae (Table 4-1) are discussed here in more detail. In each case the character number is given first, and then the character state after a hyphen. See Appendix 2 for a complete list of the characters and their states.

Node A—Tylosaurinae Williston, 1897

1-3 – edentulous rostrum on premaxilla. This character state is a unique synapomorphy of the Tylosaurinae.

3-1 – premaxilla internarial bar width equal to rostrum width. This character state is a unique synapomorphy of the Tylosaurinae.

6-1 – entrance for fifth cranial nerve removed from rostrum beneath internarial bar of premaxilla. The position of the fifth cranial nerve beneath the premaxilla has not been described for the majority of mosasaurs; the distribution of this character state on the preferred tree indicates that it could be a synapomorphy of the species of *Tylosaurus*, a synapomorphy of the tylosaurines, or even a synapomorphy of the Russellosaurina that is reversed in the Plioplatecarpini.

7-0 – free nasals present. I have followed Lingham-Soliar (1992) in coding the presence of free nasals in *Hainosaurus*; this makes distinct nasals a synapomorphy of the Tylosaurinae, convergent with *Plotosaurus bennisoni* and *Halisaurus sternbergi*. See Appendix 2 for further discussion of this character.

27-1 – prefrontal ventrally overlapping postorbitofrontal. *Hainosaurus bernardi* and *Taniwhasaurus oweni* share a unique synapomorphy: ventral overlap of the postorbitofrontal by the prefrontal. Because of the basal position of these two taxa on the preferred tree, the distribution of this character state is a synapomorphy of the Tylosaurinae. This is, however, plesiomorphic relative to the other tylosaurines, as there is contact between these elements in *Tylosaurus kansasensis* and *T. nepaeolicus* but no overlap, and in the remaining species of *Tylosaurus* the only known overlap is laterally above the orbits.

65-1 – edentulous projection of dentary. This character state is convergent with *Plotosaurus*.

108-1 – scapula half size of coracoid. This character state is convergent with *Halisaurus sternbergi*.

115-1 – lack of coracoid emargination. This character state is convergent with several taxa in the Globidensini and Mosasaurini.

116-1 – humerus greatly shortened, 1.5 to 2 times distal width. While not known from *Taniwhasaurus*, the described humeri of tylosaurines are consistently shortened. This is a synapomorphy of the Tylosaurinae, and convergent with *Halisaurus sternbergi*, but it is also possible that it is a synapomorphy of the entire Mosasauridae that is modified in the Mosasaurinae and Plioplatecarpini.

123-1 – slight anterodistal expansion of the radius. The radius is not known from *Taniwhasaurus*, but all other tylosaurines show the intermediate state of this character, making it a synapomorphy of the Tylosaurinae, convergent with *Halisaurus sternbergi*, or a synapomorphy of the entire Mosasauridae that is modified in the Mosasaurinae and Plioplatecarpini.

124-2 – centrale not ossified. For all the tylosaurines in which a well-preserved forelimb is known, the centrale is not present as an ossification. The distribution of this state on the preferred tree identifies it as a synapomorphy of the Tylosaurinae.

Node B

5-1 – dorsal keel on the internarial bar of premaxilla. This is a synapomorphy of *Taniwhasaurus oweni* and the species of *Tylosaurus*, convergent with the Plotosaurini and Bell's (1993, 1997) "*Halisaurus* n. sp." The shape of the dorsal premaxilla has not been described in *Hainosaurus*, and so the derived state may prove to be a synapomorphy for the entire Tylosaurinae.

39-1 – suprastapedial process of quadrate of moderate length, ending near middle height. This character state is a synapomorphy of this node, but its presence in *Ectenosaurus* and many mosasaurines makes it equally likely that it is plesiomorphic for the Natantia, and modified in *H. bernardi*. The character state is reversed in *T. proriger* and the crown species of *Tylosaurus*, although the 'short' suprastapedial of these taxa is of a fundamentally different nature than that of *Hainosaurus*. See Appendix 2 for further discussion of this character.

40-2 – tapered suprastapedial process of quadrate. An unconstricted suprastapedial process with a tapered profile is a unique synapomorphy for all tylosaurines in which a well-preserved quadrate is known. The small suprastapedial of *Hainosaurus bernardi* (Lingham-Soliar, 1992:fig. 9) is certainly not constricted, but does not match the parallel-sided form typical of *Platecarpus* and *Plioplatecarpus*, nor the tapered form typical of *Tylosaurus*, and has been coded missing for this character. Given the concerns about the preservation of the quadrate of *H. bernardi* (Russell, 1967:176), future work may demonstrate that a tapered suprastapedial process is synapomorphic for the entire Tylosaurinae. See Appendix 2 for further discussion of this character.

Node C—*Tylosaurus* Marsh, 1872

33-0 – exclusion of prefrontal from margin of external naris. Caldwell et al.'s (2005) observation that the prefrontal contributes to the narial margin in *Taniwhasaurus* makes it possible that prefrontal exclusion is a synapomorphy of *Tylosaurus*, convergent in *Plotosaurus* and *Ectenosaurus*, but as Bell (1993:79) observed it is also possible that state 0 is a synapomorphy of the Russellosaurina, reversing in the Plioplatecarpini and

Taniwhasaurus, and still convergent in *Plotosaurus*. See Appendix 2 for further discussion of this character.

36-1 – ectopterygoid contact with the maxilla. The ectopterygoid is undescribed for all the tylosaurines not included by Bell (1997). The presence of the derived state in *Tylosaurus kansasensis* and *T. nepaeolicus* suggests that it may be a synapomorphy of the species of *Tylosaurus*, reversed in *T. proriger*, or even a synapomorphy of the Tylosaurinae. This state is convergent with Bell's (1997) *Platecarpus* aff. *somenensis*.

58(1) – upward deflection of ventral condyle on anterior face of quadrate. The distribution of state 1 of this character is unequivocally restricted to the species of *Tylosaurus*, but it is not unique to these taxa, and it is equally parsimonious to follow Bell (1993) and consider it a synapomorphy of the Natantia that reverses in *Hainosaurus bernardi*, *Taniwhasaurus oweni*, and the Plotosaurini.

63-4 – 13 dentary teeth. The distribution of state 4 of this character, thirteen dentary teeth, is unequivocally restricted to the species of *Tylosaurus* within the Tylosaurinae, convergent with Bell's (1993, 1997) *Ectenosaurus* composite YP.

Node D

4-1 – rectangular internarial bar base. This state is a unique synapomorphy of the species of *Tylosaurus*, save for *T. kansasensis* (Everhart, 2005:235).

61-1 – anteroposteriorly elongate basioccipital basal tubera. Though the morphology of the basioccipital is not known from *Tylosaurus saskatchewanensis* (Chapter 3), the derived condition of this character appears to be a unique synapomorphy of *T. nepaeolicus* and the crown species of *Tylosaurus*.

84-1 – serration of tooth carinae. Serrated tooth carinae are a synapomorphy of *T. nepaeolicus* and the crown species of *Tylosaurus*, convergent with several species of *Prognathodon* and *Mosasaurus*.

Node E

27-2 – lateral overlap of prefrontal by postorbitofrontal. A lateral overlap of the prefrontal by the postorbitofrontal above the orbits is characteristic of *Tylosaurus proriger* and the other crown species of *Tylosaurus*. This character state is convergent with *Plesiotylosaurus crassidens*, although in *Plesiotylosaurus* the anterior process of the postorbitofrontal is short, and it does not rest in a groove in the prefrontal (Bell, 1997:307).

71-1 – medial wing of coronoid contacts angular. The medial morphology of the coronoid is only known from the tylosaurine species originally described by Bell (1993, 1997). *Tylosaurus kansasensis* and *T. nepaeolicus* share the primitive condition, and the derived state could either be a synapomorphy of the other *Tylosaurus* species or an autapomorphy of *T. proriger*.

132-2 – reduced pubic tubercle. In *Tylosaurus proriger* and the two species in this thesis, the pubic tubercle is reduced to a low ridge. This state may be a synapomorphy of these species, but because the pubis is not known from the other tylosaurines, it could also be a synapomorphy of the Tylosaurinae.

Node F

94-1 – anterior termination of zygopophyses. In *T. proriger* vertebral zygopophyses extend backward as far as the sacral region. In *T. pembinensis* zygopophyses become obsolete early in the dorsal series (Chapter 2), and in *T. saskatchewanensis* they extend only half the length of the dorsal series (Chapter 3). This is convergent with the two species of *Plotosaurus*.

109-2 – extreme widening of scapula. This character state is a synapomorphy of *Tylosaurus pembinensis* and *T. saskatchewanensis*, convergent with *Mosasaurus maximus* and *Plotosaurus tuckeri*. See Appendix 2 for further discussion of this character.

Phylogenetic Results Within the Tylosaurinae

Hainosaurus and *Taniwhasaurus* are placed basally in the Tylosaurinae, with weak support for the position of *Hainosaurus* as sister group to all other tylosaurines. This is contrary to Bell's (1997:321) suggestion that inclusion of *Hainosaurus* would make *Tylosaurus* paraphyletic. Bell's (1997) *Tylosaurus* novum sp., now known as *T. kansasensis* (Everhart, 2005), is the most basal member of *Tylosaurus*, followed by *T. nepaeolicus*, then *T. proriger*, and with *T. pembinensis* and *T. saskatchewanensis* at the crown of the clade; this is in complete agreement with the stratigraphic occurrence of these taxa. While branch support for the Tylosaurinae (Node A) is robust, resolution amongst the tylosaurine taxa is poor (Fig. 4-3).

Monophyly of the Tylosaurinae is supported by several synapomorphies: edentulous extensions of the premaxilla and dentary (characters 1-3 and 65-1), a scapula that is half the size of the coracoid (character 108-1), a lack of coracoid emargination (character 115-1), a shortened humerus (character 116-1), and the lack of an ossified centrale in the manus (character 124-2). All of these are known from previous treatments of tylosaurine systematics (Russell, 1967; Bell, 1993). The inclusion of additional tylosaurine taxa in this analysis has shown that some of the characters identified by Bell (1993, 1997) as characteristics of *Tylosaurus* are diagnostic of the entire Tylosaurinae. This includes an internarial bar of the premaxilla that is the same width as the rostrum (character 3-1), and slight anterodistal expansion of the radius (character 123-1). A new synapomorphy, ventral overlap of the postorbitofrontal by the prefrontal (character 27-1), diagnoses the Tylosaurinae, but is plesiomorphic relative to the species of *Tylosaurus*. Two other apomorphies are tentatively assigned to this node, but cannot be confirmed because they are missing from the majority of taxa: posterior position of the entrance for the fifth cranial nerve beneath the premaxilla (character 6-1), and the presence of free nasals (character 7-0).

The primitive position of *Hainosaurus bernardi* and *Taniwhasaurus oweni* is supported by a pair of synapomorphies: ventral overlap of the postorbitofrontal by the prefrontal, and the lack of an upward deflection of the ventral condyle on the anterior face of the quadrate. Contribution of the prefrontal to the margin of the external nares has been observed in *Taniwhasaurus oweni* (Welles and Gregg, 1971; Caldwell et al., 2005) and may also be characteristic of basal tylosaurines, but has yet to be confirmed in *H. bernardi* (see discussion in Chapter 2).

The node including all tylosaurines save *Hainosaurus* (Node B) is supported by a single synapomorphy: a moderately-long suprastapedial process (character 39-1), though this character is reversed at Node E. Two other synapomorphies of this clade, a dorsal keel on the premaxilla (character 5-1) and an unconstricted suprastapedial with a tapered profile (character (40-2), are coded missing for *Hainosaurus bernardi*, and are likely to change their status following a clarification of the anatomy of this taxon. The basal position of *H. bernardi* within the Tylosaurinae is thus rather weakly supported, and this explains the poor branch support for Node B (Fig. 4-3).

The monophyly of genus *Tylosaurus* (Node C) is supported by two synapomorphies: the upward deflection of the ventral condyle onto the anterior face of the quadrate (character 58-1), and 13 dentary teeth (character 63-4). Exclusion of the prefrontal from the narial margin (character 33-0) is also likely to prove a synapomorphy at this node; its absence in *H. bernardi* is uncertain (see discussion in Chapter 2). Contact between the ectopterygoid and the maxilla (character 36-1) is coded only for the species of *Tylosaurus* from Bell's (1993, 1997) analysis, and the status of this synapomorphy is difficult to evaluate.

The clade containing all the species of *Tylosaurus* except *T. kansasensis* (Node D) is united by three synapomorphies: a rectangular cross section at the origin of the premaxillary internarial bar (character 4-1), anteroposteriorly elongate basal tubera of the basioccipital (character 61-1), and serrated tooth carinae (character 84-1). The recent description of *T. kansasensis* confirms the absence of the first and last character states in this taxon (Everhart, 2005:235).

The node comprising *Tylosaurus proriger*, *T. pembinensis*, and *T. saskatchewanensis* (Node E) is supported by two synapomorphies: lateral overlap of the prefrontal by the postorbitofrontal (character 27-2), and slight anterodistal expansion of the radius (character 123-2). Contact between the medial wing of the coronoid and the angular (character 71-1) is also coded only for Bell's *Tylosaurus* species, and it is not certain whether this is a synapomorphy for this clade.

The two species of *Tylosaurus* described in Chapters 2 and 3 are positioned at the crown of the Tylosaurinae by a pair of synapomorphies: anterior termination of the zygopophyses (character 94-1), and extreme anteroposterior widening of the scapula (character 109-2). The status of the first character is questionable, however, because the extent of the zygopophyses is only coded for these two taxa and *T. proriger*, amongst the Tylosaurinae.

The basal position of *H. bernardi* is incongruent with its geological occurrence in the Early Maastrichtian, but a number of missing characters make its phylogenetic position far from certain. *Taniwhasaurus oweni*, from the Early to Middle Campanian, is also considerably younger than the earliest species of *Tylosaurus* in the late Coniacian, but there is no doubt that the anatomy of this species is primitive compared to *T. kansasensis* and *T. nepaeolicus*. Support for the basal positions in the clade is far from robust, but separation of *Hainosaurus* from the species of *Tylosaurus* confirms that the generic assignments of *T. pembinensis* and *T. saskatchewanensis* are correct.

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TABLE 4-1. Character transformations supporting the labelled nodes of the majority-rule consensus tree (Fig. 4-3), with the character number and the state after the hyphen. Unequivocal transformations are preceded by U, and equivocal transformations by E.

Node	Characters and states
A	U1-3, U3-1, E6-1, 7-0, 27-1, U65-1, U108-1, 115-1, 116-1, 123-1, 124-2, E136-1
B	5-1, 39-1, 40-2
C	33-0, E36-1, 58-1, U63-4
D	4-1, 61-1, 84-1
E	27-2, E71-1, 123-2
F	94-1, 109-2

FIGURE 4-1. Bell's (1997) preferred phylogeny of the Mosasauroidea, a strict consensus tree of 99 equally parsimonious trees of length 351 steps.

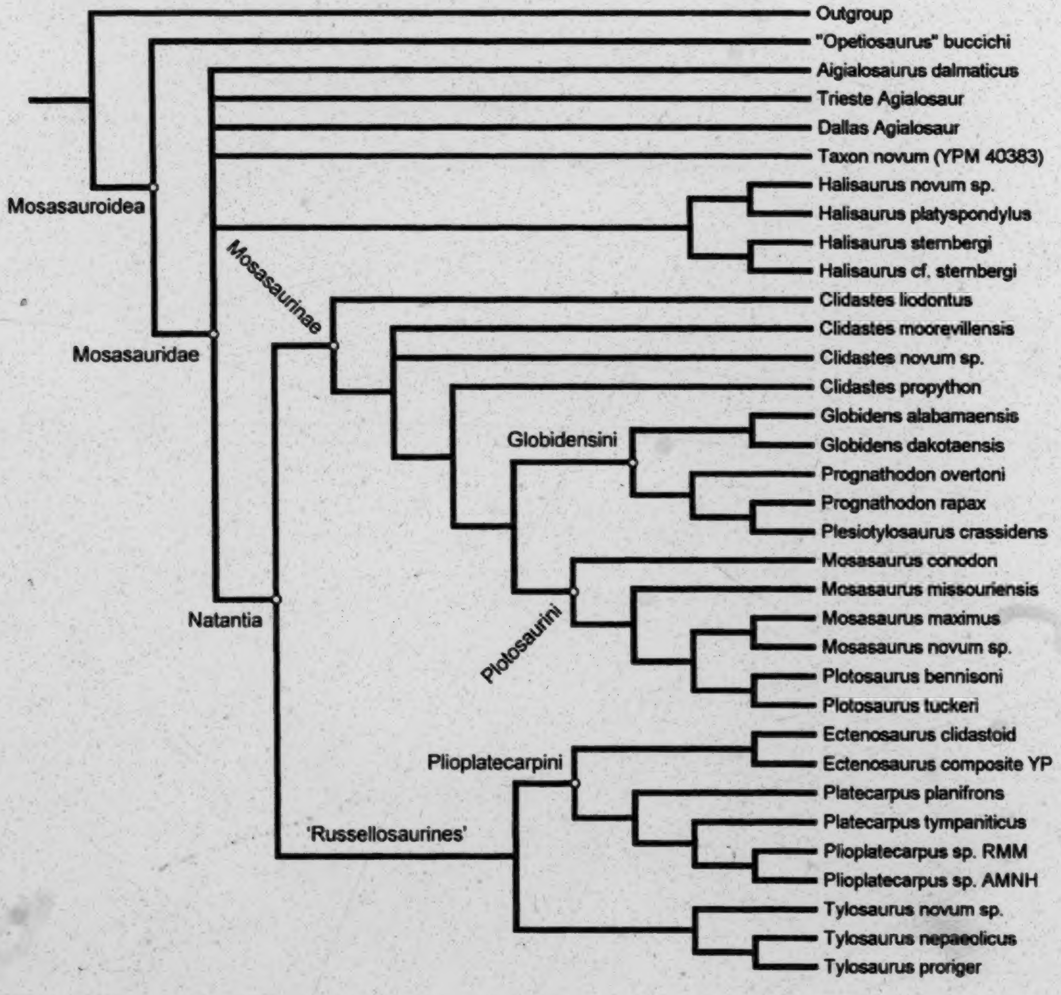

Outgroup
"Opetiosaurus" buccichi
Aigialosaurus dalmaticus
Trieste Agialosaur
Dallas Agialosaur
Taxon novum (YPM 40383)
Halisaurus novum sp.
Halisaurus platyspondylus
Halisaurus sternbergi
Halisaurus cf. sternbergi
Clidastes liodontus
Clidastes moorevillensis
Clidastes novum sp.
Clidastes propython
Globidens alabamaensis
Globidens dakotaensis
Prognathodon overtoni
Prognathodon rapax
Plesiotylosaurus crassidens
Mosasaurus conodon
Mosasaurus missouriensis
Mosasaurus maximus
Mosasaurus novum sp.
Plotosaurus bennisoni
Plotosaurus tuckeri
Ectenosaurus clidastoid
Ectenosaurus composite YP
Platecarpus planifrons
Platecarpus tympaniticus
Plioplatecarpus sp. RMM
Plioplatecarpus sp. AMNH
Tylosaurus novum sp.
Tylosaurus nepaeolicus
Tylosaurus proriger
Mosasauroidea
Mosasauridae
Mosasaurinae
Natantia
Globidensini
Plotosaurini
Plioplatecarpini
'Russellosaurines'

FIGURE 4-2. Phylogeny of the Mosasauroidea based on parsimony analysis of 136 unordered morphological characters. Strict consensus of 54 shortest trees (length = 338, CI = 0.494, RI = 0.804, HI = 0.506).

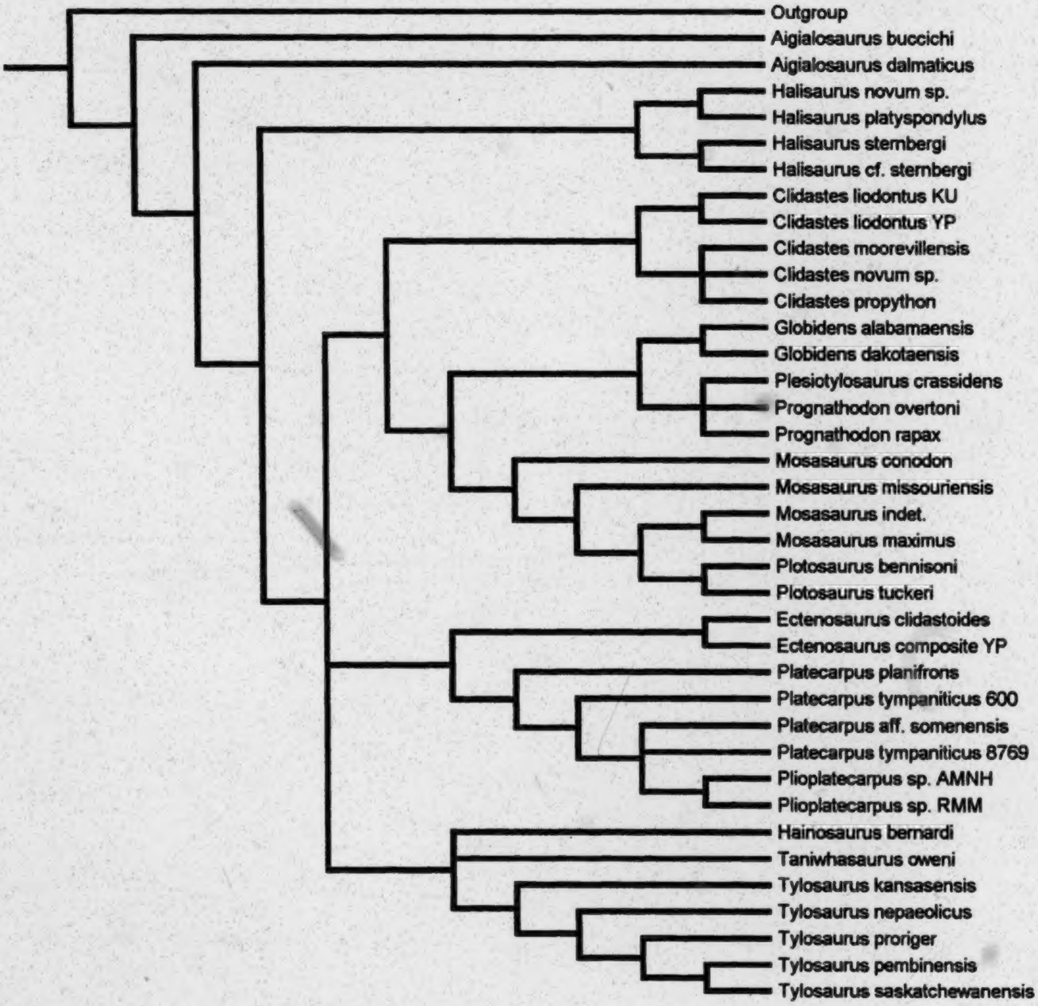
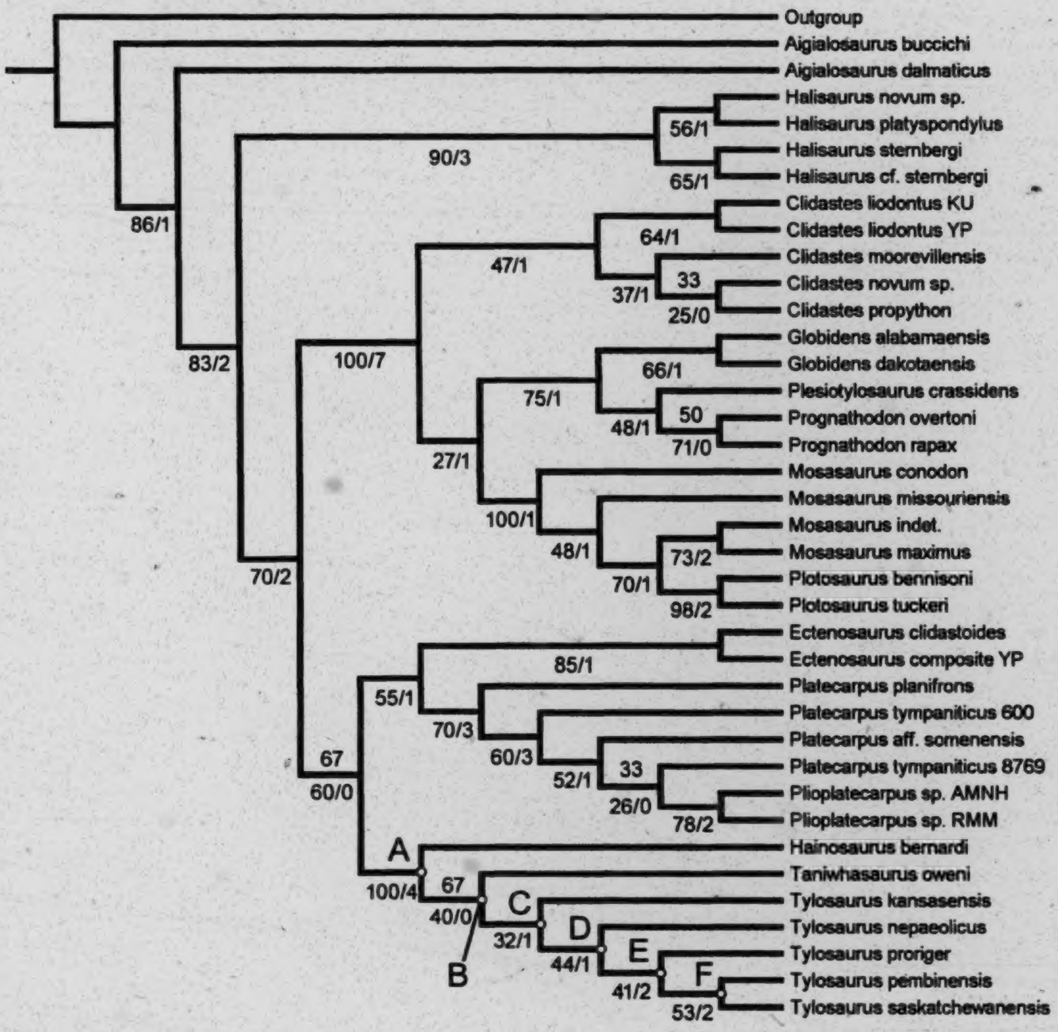

Outgroup
Aigialosaurus buccichi
Aigialosaurus dalmaticus
Halisaurus novum sp.
Halisaurus platyspondylus
Halisaurus sternbergi
Halisaurus cf. sternbergi
Clidastes liodontus KU
Clidastes liodontus YP
Clidastes moorevillensis
Clidastes novum sp.
Clidastes propython
Globidens alabamaensis
Globidens dakotaensis
Plesiotylosaurus crassidens
Prognathodon overtoni
Prognathodon rapax
Mosasaurus conodon
Mosasaurus missouriensis
Mosasaurus indet.
Mosasaurus maximus
Plotosaurus bennisoni
Plotosaurus tuckeri
Ectenosaurus clidastoides
Ectenosaurus composite YP
Platecarpus planifrons
Platecarpus tympaniticus 600
Platecarpus aff. somenensis
Platecarpus tympaniticus 8769
Plioplatecarpus sp. AMNH
Plioplatecarpus sp. RMM
Hainosaurus bernardi
Taniwhasaurus oweni
Tylosaurus kansasensis
Tylosaurus nepaeolicus
Tylosaurus proriger
Tylosaurus pembinensis
Tylosaurus saskatchewanensis

FIGURE 4-3. Phylogeny of the Mosasauroidea based on parsimony analysis of 136 unordered morphological characters. Majority-rule consensus of 54 shortest trees (length = 338, CI = 0.494, RI = 0.804, HI = 0.506), showing all compatible groupings. Numbers above the branch are the percentage of shortest trees compatible with each node; remaining nodes are present in all shortest trees. Numbers below the branch indicate the bootstrap frequency and Bremer support value for each node.


Outgroup
Aigialosaurus buccichi
Aigialosaurus dalmaticus
Halisaurus novum sp.
Halisaurus platyspondylus
56/1
Halisaurus sternbergi
90/3
Halisaurus cf. sternbergi
65/1
Clidastes liodontus KU
86/1
Clidastes liodontus YP
64/1
Clidastes moorevillensis
47/1
33
Clidastes novum sp.
37/1
Clidastes propython
25/0
Globidens alabamaensis
83/2
100/7
Globidens dakotaensis
66/1
Plesiotylosaurus crassidens
75/1
50
Prognathodon overtoni
48/1
Prognathodon rapax
71/0
27/1
Mosasaurus conodon
Mosasaurus missouriensis
100/1
Mosasaurus indet.
48/1
73/2
Mosasaurus maximus
70/2
Plotosaurus bennisoni
70/1
Plotosaurus tuckeri
98/2
Ectenosaurus clidastoides
85/1
Ectenosaurus composite YP
55/1
Platecarpus planifrons
Platecarpus tympaniticus 600
70/3
Platecarpus aff. somenensis
60/3
67
33
Platecarpus tympaniticus 8769
52/1
60/0
Plioplatecarpus sp. AMNH
26/0
78/2
Plioplatecarpus sp. RMM
A
Hainosaurus bernardi
67
Taniwhasaurus oweni
100/4
C
Tylosaurus kansasensis
40/0
D
Tylosaurus nepaeolicus
32/1
E
Tylosaurus proriger
44/1
F
Tylosaurus pembinensis
B
41/2
53/2
Tylosaurus saskatchewanensis

APPENDIX 1

Taxon	Character number					
	5	10	15	20	25	30
Outgroup	00000	00?0?	?00??	?0000	0??00	0?00?
Aigialosaurus dalmaticus	??0?0	?1110	??0??	?1?10	?10?0	0?00?
Aigialosaurus buccichi	?00??	??110	??0??	?10?0	??0??	0?0??
Clidastes liodontus KU	21000	?1101	0?101	01001	111?1	0?102
Clidastes liodontus YP	21000	?1101	??101	01001	?11?1	0?102
Clidastes moorevillensis	21000	01101	00101	01001	111?1	0?102
Clidastes novum sp.	21000	01101	0?101	01001	11111	0?102
Clidastes propython	21000	??101	00101	01001	11??1	0?102
Ectenosaurus clidastoides	210?0	?1101	??102	01110	?01?0	0?011
Ectenosaurus composite YP	11000	1?1??	11102	01110	0?1??	??0??
Globidens alabamaensis	?????	??0?1	10101	?????	????1	0?10?
Globidens dakotaensis	210?0	?1011	??101	01001	?11?1	1?104
Hainosaurus bernardi	311??	?0011	??1??	?1002	?11?0	110?4
Halisaurus novum sp.	11001	0?100	0000?	?????	????0	0???0
Halisaurus platyspondylus	11000	0?110	0000?	?1010	1?0?0	0????
Halisaurus sternbergi	?????	?0110	??0??	?0010	?0000	0???0
Halisaurus cf. *sternbergi*	0100?	0???0	0000?	?0011	100??	0???0
Mosasaurus conodon	?????	?????	?????	?????	?????	?????
Mosasaurus indet.	210?1	?1101	??101	11001	?11?1	1?003

Mosasaurus maximus	21001	?1001	??101	11002	111?1	10003
Mosasaurus missouriensis	21001	?1001	??101	11001	?11?1	1?003
Platecarpus planifrons	11000	01011	1?100	?1110	?11?0	0??15
Platecarpus aff. *somenensis*	?????	??011	??100	?1112	?11?0	100?5
Platecarpus tympaniticus 8769	01000	0?011	11100	?1111	011?0	10015
Platecarpus tympaniticus 600	110?0	?1011	??100	?1110	??1?0	10015
Plesiotylosaurus crassidens	210?0	?1101	??101	11001	?11?1	12104
Plioplatecarpus sp. AMNH	?????	??011	??100	?1113	011?0	1000?
Plioplatecarpus sp. RMM	?????	??0?1	00100	?1113	011??	??0??
Plotosaurus bennisoni	11001	?0011	??101	11011	?1111	1?001
Plotosaurus tuckeri	110?1	??011	??101	11011	?1111	1?001
Prognathodon overtoni	11000	??001	00101	11001	?1111	1?105
Prognathodon rapax	11000	??001	00101	11001	111?1	1?1?4
Taniwhasaurus oweni	311?1	??011	??1??	?????	????0	11??3
Tylosaurus kansasensis	31101	10011	01101	11001	?11?0	1?014
Tylosaurus nepaeolicus	31111	?0011	0111?	?1000	?1110	1?004
Tylosaurus pembinensis	31111	??011	011??	?1001	?11?0	12004
Tylosaurus proriger	31111	10011	?111?	?1001	?1110	12004
Tylosaurus saskatchewanensis	31111	??001	??1??	?1001	?1110	12005

Taxon	Character number					
	35	40	45	50	55	60
Outgroup	0?10?	000??	?0???	000?0	00000	0?0?0
Aigialosaurus dalmaticus	??100	???2?	?0???	1?00?	00???	??000
Aigialosaurus buccichi	0??00	???2?	?0???	??00?	00???	?????
Clidastes liodontus KU	1012?	?1010	?0000	00100	01000	00101
Clidastes liodontus YP	101??	?1010	?0000	00100	01000	00101
Clidastes moorevillensis	1?120	?1010	?0010	10100	01000	00101
Clidastes novum sp.	10120	01010	?0010	10100	01000	001?1
Clidastes propython	1?1??	?1010	?0010	10100	01000	00101
Ectenosaurus clidastoides	10011	?0010	01?11	0110?	11000	???10
Ectenosaurus composite YP	0??11	00010	01211	01100	?1000	???1?
Globidens alabamaensis	1????	?1010	?1111	?0?00	?1000	001??
Globidens dakotaensis	10120	?1010	?1011	10100	01001	001?1
Hainosaurus bernardi	00?10	?000?	?020?	01100	01000	000?0
Halisaurus novum sp.	??1??	?1?20	01010	0????	?0000	10??0
Halisaurus platyspondylus	11???	?1?20	01010	00000	00000	100??
Halisaurus sternbergi	2111?	??020	?1??0	0000?	01???	10???
Halisaurus cf. *sternbergi*	2????	?00??	?????	?????	?????	?????
Mosasaurus conodon	?????	?????	?????	?????	?????	?????
Mosasaurus indet.	101??	?1?00	?001?	01010	10111	10001
Mosasaurus maximus	1??21	?1000	?0010	01010	10111	100?1

Mosasaurus missouriensis	101??	?1000	?0010	00100	11011	100?1
Platecarpus planifrons	001?1	00021	00110	00100	00001	101?0
Platecarpus aff. *somenensis*	0??11	10021	10?11	00100	00101	101?0
Platecarpus tympaniticus 8769	00111	?0021	10111	00100	00101	101?0
Platecarpus tympaniticus 600	?0111	?0021	10111	00100	00101	10110
Plesiotylosaurus crassidens	11???	?1110	?1011	101??	01???	101??
Plioplatecarpus sp. AMNH	0??11	00021	10??2	00100	00101	111?0
Plioplatecarpus sp. RMM	?????	?0021	10012	00100	?0100	11???
Plotosaurus bennisoni	10020	01000	?0010	00010	11011	10001
Plotosaurus tuckeri	100?0	?1000	?0010	00010	11??1	100?1
Prognathodon overtoni	00?20	?1110	?1011	10?01	?1000	001?1
Prognathodon rapax	1?120	?1110	?1011	10101	01000	10101
Taniwhasaurus oweni	?0111	?0012	?011?	11100	01000	000??
Tylosaurus kansasensis	10021	10012	?0200	11100	01001	00110
Tylosaurus nepaeolicus	0???1	10012	?0210	11100	01000	00110
Tylosaurus pembinensis	00011	?0002	?0210	00100	01000	00110
Tylosaurus proriger	10011	00002	?0210	00100	01000	00110
Tylosaurus saskatchewanensis	00011	???02	?0210	00100	01000	001??

	Character number					
Taxon	65	70	75	80	85	90
Outgroup	00?00	0??00	00000	?0?00	00?00	0?000
Aigialosaurus dalmaticus	0????	1??0?	??010	0??00	0020?	?010?
Aigialosaurus buccichi	??000	0??00	0?0??	0?000	00200	?????
Clidastes liodontus KU	00200	22?10	00100	0?101	00201	01100
Clidastes liodontus YP	0?100	2??10	?01??	??101	00201	0110?
Clidastes moorevillensis	00200	22010	00100	00101	00201	01100
Clidastes novum sp.	0?200	22010	00100	00101	00201	0110?
Clidastes propython	00100	2201?	10100	00101	00201	01100
Ectenosaurus clidastoides	0?3??	20?1?	00000	?1001	10201	??100
Ectenosaurus composite YP	?1400	2001?	?0000	01001	10201	001??
Globidens alabamaensis	?????	?2010	?1100	00110	01101	011??
Globidens dakotaensis	00???	?????	?????	??110	01101	011?0
Hainosaurus bernardi	0?301	???00	??000	00001	002?1	000?0
Halisaurus novum sp.	0001?	12011	00010	00100	00100	??0?0
Halisaurus platyspondylus	?????	?201?	00010	00100	00101	??0??
Halisaurus sternbergi	?????	1??1?	??010	00???	?????	?10??
Halisaurus cf. *sternbergi*	?0?1?	120??	0?010	0010?	00100	?????
Mosasaurus conodon	??1??	2201?	???00	00101	00211	01110
Mosasaurus indet.	0??00	220??	????1	??101	00211	010??
Mosasaurus maximus	00300	22010	?1101	10101	00211	01110

Mosasaurus missouriensis	0?300	2?010	11101	10101	002?1	011?0
Platecarpus planifrons	01500	22001	00000	01001	10201	10100
Platecarpus aff. *somenensis*	0?51?	2??01	00000	01001	00201	100??
Platecarpus tympaniticus 8769	0151?	22101	00000	?1001	00201	100?0
Platecarpus tympaniticus 600	0151?	22101	00000	0?001	00201	1011?
Plesiotylosaurus crassidens	??200	2??10	1?100	??1?0	002?1	?????
Plioplatecarpus sp. AMNH	0?51?	22101	00000	01???	?0??1	?????
Plioplatecarpus sp. RMM	01???	?21??	??000	11001	0020?	??0??
Plotosaurus bennisoni	0?101	?2?1?	??101	10000	012??	010?1
Plotosaurus tuckeri	0?101	2??11	1?101	?0???	????1	????1
Prognathodon overtoni	00300	21010	11100	10110	01211	?????
Prognathodon rapax	00?1?	21010	???00	00110	01211	0110?
Taniwhasaurus oweni	??201	???00	?0???	??001	002?1	000??
Tylosaurus kansasensis	00401	22000	00000	00001	00201	00110
Tylosaurus nepaeolicus	1?401	22000	00000	00001	00211	000?0
Tylosaurus pembinensis	10401	22000	??000	00001	00211	000?0
Tylosaurus proriger	10401	22000	10000	00001	00211	100?0
Tylosaurus saskatchewanensis	??401	?2000	??000	00?01	00211	000?0

Taxon	Character number					
	95	100	105	110	115	120
Outgroup	?0000	?00?0	?00?0	0000?	?0000	00000
Aigialosaurus dalmaticus	?000?	???00	00???	??00?	0????	000?0
Aigialosaurus buccichi	000?0	???00	?0000	0000?	00?00	0000?
Clidastes liodontus KU	00001	20101	?1111	01011	01000	21001
Clidastes liodontus YP	00001	20101	?1???	?????	?????	21001
Clidastes moorevillensis	00001	2?101	?1111	??011	01000	21001
Clidastes novum sp.	00?01	2110?	??1?1	??011	01000	21001
Clidastes propython	00001	2?10?	??1?1	?????	??000	21001
Ectenosaurus clidastoides	10001	???0?	?????	??010	11100	21??0
Ectenosaurus composite YP	?????	?????	?????	?????	??1??	?????
Globidens alabamaensis	0?0?1	2??0?	?????	?????	?10??	21001
Globidens dakotaensis	0?0?1	2?10?	?????	?????	?????	?????
Hainosaurus bernardi	????1	10??1	????0	??1?0	?1??1	1????
Halisaurus novum sp.	00100	00100	?1??1	?????	?????	?????
Halisaurus platyspondylus	????0	0????	????1	?????	?????	?????
Halisaurus sternbergi	00100	???00	11101	01111	11100	10000
Halisaurus cf. *sternbergi*	?????	0????	?????	?????	?????	?????
Mosasaurus conodon	010?1	2011?	????1	???1?	01010	31101
Mosasaurus indet.	?10?1	2??1?	?????	????1	010??	31101
Mosasaurus maximus	11001	20?1?	?1111	??021	01011	31101

Mosasaurus missouriensis	000?1	20111	?1??1	??01?	?100?	?????
Platecarpus planifrons	000?1	1??0?	?????	??010	11100	20?10
Platecarpus aff. *somenensis*	??0??	1????	?????	?????	?????	?????
Platecarpus tympaniticus 8769	000?1	1??0?	????0	?????	?????	?????
Platecarpus tympaniticus 600	00001	10000	01000	10010	11100	20?1?
Plesiotylosaurus crassidens	00001	2?10?	?????	??011	01011	31201
Plioplatecarpus sp. AMNH	?????	?????	?????	??010	11100	20?10
Plioplatecarpus sp. RMM	00001	10000	????0	?????	?????	?????
Plotosaurus bennisoni	0?011	2??1?	?????	?????	?????	?????
Plotosaurus tuckeri	01011	20111	???1?	??021	01011	31101
Prognathodon overtoni	?0??1	2????	????1	?????	?????	21201
Prognathodon rapax	00001	2110?	????1	??01?	01011	21201
Taniwhasaurus oweni	?????	?????	????0	??110	0110?	?????
Tylosaurus kansasensis	0?0??	1??0?	?????	??110	11101	10?10
Tylosaurus nepaeolicus	000?1	100??	?????	?????	?????	10??0
Tylosaurus pembinensis	00?11	1000?	????0	??120	01101	10?10
Tylosaurus proriger	00001	10000	11000	10110	11101	10?10
Tylosaurus saskatchewanensis	00011	10001	????0	??120	11101	10?10

Taxon	Character number			
	125	130	135	140
Outgroup	00000	00000	000?0	0
Aigialosaurus dalmaticus	00000	00000	01??0	0
Aigialosaurus buccichi	00000	0000?	???0	0
Clidastes liodontus KU	11210	00101	00012	0
Clidastes liodontus YP	11210	0010?	????2	?
Clidastes moorevillensis	11210	00101	00012	0
Clidastes novum sp.	11210	0010?	????2	?
Clidastes propython	11210	?0???	????2	?
Ectenosaurus clidastoides	01201	0100?	????1	0
Ectenosaurus composite YP	?????	?????	?????	?
Globidens alabamaensis	11???	?????	????2	?
Globidens dakotaensis	?????	?????	?????	?
Hainosaurus bernardi	00121	1?00?	?????	?
Halisaurus novum sp.	?????	?????	?????	?
Halisaurus platyspondylus	?????	?????	1????	?
Halisaurus sternbergi	00101	11001	111?0	0
Halisaurus cf. *sternbergi*	?????	?????	?????	?
Mosasaurus conodon	11?1?	?????	????2	?
Mosasaurus indet.	11210	0011?	????2	?
Mosasaurus maximus	11210	00111	00012	1

Mosasaurus missouriensis	??210	0?11?	????2	?
Platecarpus planifrons	0?201	1100?	????1	?
Platecarpus aff. *somenensis*	?????	?????	??1??	?
Platecarpus tympaniticus 8769	?????	?????	?????	?
Platecarpus tympaniticus 600	01201	11001	01101	0
Plesiotylosaurus crassidens	11210	0010?	????2	?
Plioplatecarpus sp. AMNH	01201	1100?	????1	?
Plioplatecarpus sp. RMM	?????	?????	?????	?
Plotosaurus bennisoni	?????	?????	?????	?
Plotosaurus tuckeri	11210	0011?	????2	1
Prognathodon overtoni	?1???	?????	?????	?
Prognathodon rapax	11210	0010?	????2	?
Taniwhasaurus oweni	?????	?????	?????	?
Tylosaurus kansasensis	001??	?????	????1	?
Tylosaurus nepaeolicus	001?1	1100?	?????	?
Tylosaurus pembinensis	001??	?1001	020?1	?
Tylosaurus proriger	00121	11001	02001	1
Tylosaurus saskatchewanensis	00121	11001	02001	?

APPENDIX 2

Morphological characters and states used in the phylogenetic analysis. Data set is modified from Bell (1997); see his descriptions as well as those of Bell (1993); changes and additions are noted. Numbers in square brackets correspond to the character numbers from Bell's (1997) original matrix.

Skull Characters

(1) [1,2] Premaxilla predental rostrum: total lack of bony rostrum (0); rostrum either very short or obtuse (1); or distinctly protruding (2); or very large and inflated (3). Bell's (1997) first two characters were [1] a binary character describing the presence or absence of a premaxillary rostrum, and [2] a three-state character describing the shape of the premaxillary rostrum. These have been combined into a single character which avoids the necessity of scoring [2] as missing data for all taxa that lack a premaxillary rostrum.

(2) [3] Premaxilla shape: bone broadly arcuate anteriorly (0); or relatively narrowly arcuate or acute anteriorly (1).

(3) [4] Premaxilla internarial bar width: narrow, distinctly less than half of maximum width of rostrum in dorsal view (0); or wide, being barely narrow than rostrum (1).

(4) [5] Premaxilla internarial bar base shape: triangular (0); or rectangular (1).

(5) [6] Premaxilla internarial bar dorsal keel: absent (0); or present (1).

(6) [7] Premaxilla internarial bar venter: with entrance for fifth cranial (facial) nerve close to rostrum (0); or far removed from rostrum (1).

(7) [8] Nasals: present (0); or absent or fused to other elements (1). Mosasaur nasals have been reported from *Plotosaurus bennisoni* (Camp, 1942:4), *Tylosaurus "dyspelor"* (=*T. proriger*) (Huene, 1910:303), and *Halisaurus sternbergi* (Wiman, 1920:15). Lingham-Soliar (1992) reported free nasals in the referred specimen of *Hainosaurus bernardi*, and a specimen of *Tylosaurus* sp. Bell (1993) could not confirm the presence of nasals in any specimen of *Tylosaurus* he observed but coded them present; this has been followed here. The nasals are either consistently removed by taphonomic processes, indistinguishably fused to the adjoining bones during ontogeny, or have been lost at some point in the phylogeny of mosasaurids.

(8) [10] Frontal width: element broad and short (0); or long and narrow (1).

(9) [11] Frontal narial emargination: frontal not invaded by posterior end of nares (0); or distinct embayment present (1).

(10) [13] Frontal ala shape: sharply acuminate (0); or more broadly pointed or rounded (1).

(11) [14] Frontal olfactory canal embrasure: canal not embraced centrally by descending process (0); or canal almost or completely enclosed below (1).

(12) [16] Frontal posteroventral midline: tabular boss immediately anterior to frontal-parietal suture absent (0); or present (1).

(13) [17] Frontal-parietal suture: opposing surfaces with low interlocking ridges (0); or with overlapping flanges (1).

(14) [18] Frontal-parietal suture overlap orientation: suture with oblique median frontal and parietal ridges contributing to overlap (0); or with all three ridges almost horizontal (1).

(15) [19] Frontal invasion of parietal: lateral surface flange of frontal posteriorly extended (0); or median frontal sutural flange posteriorly extended (1); or both extended (2).

(16) [20] Frontal median invasion of parietal II: if present posteriorly extended median sutural ridge short (0); or long (1).

(17) [21] Parietal length: dorsal surface relatively short with epaxial musculature insertion posterior between suspensorial rami only (0); or dorsal surface elongate with epaxial musculature insertion dorsal as well as posterior (1).

(18) [22] Parietal table shape: generally rectangular to trapezoidal with sides converging but not meeting (0); or triangular with straight sides contacting in front of suspensorial rami (1).

(19) [23] Parietal foramen size: relatively small (0); or large (1).

(20) [24] Parietal foramen position I: foramen generally nearer to center of parietal table, well away from frontal-parietal (0); or close to suture (1); or touching suture (2); or huge foramen straggling suture and deeply invading frontal (3). Bell (1997) modified the states of this character from those of his original matrix (Bell, 1993), combining a state for touching the suture with a state for close to the suture, but did not change their coding in the matrix. This original distinction is a useful one, since state 1 as stated by Bell (1997) covers a considerable range of foramen positions: from contacting the frontal at the suture to being wholly within the parietal up to a foramen's length from the suture. To reflect this difference I have restored the original character states.

(21) [25] Parietal foramen ventral opening: level with main ventral surface (0); or surrounded by rounded, elongate ridge (1).

(22) [26] Parietal posterior shelf: presence of distinct horizontal shelf projecting posteriorly from between suspensorial rami (0), or shelf absent (1).

(23) [27] Parietal suspensorial ramus compression: greatest width vertical or oblique (0); or greatest width horizontal (1).

(24) [28] Parietal union with supratemporal: suspensorial ramus from parietal overlapping supratemporal without interdigitation (0); or forked distal ramus sandwiches end of supratemporal (1).

(25) [29] Prefrontal supraorbital process: process absent, or present as very small rounded knob (0); or present as distinct to large, triangular or rounded, overhanging wing (1).

(26) [30] Prefrontal contact with postorbitofrontal: no contact at edge of frontal (0); or elements in contact there (1).

(27) [31] Prefrontal-postorbitofrontal overlap: prefrontal overlapped ventrally by postorbitofrontal (0); postorbitofrontal ventrally overlapped by prefrontal (1); or prefrontal overlapped laterally (2). The condition of the prefrontal-postorbitofrontal contact in *Taniwhasaurus oweni* (Caldwell et al., 2005:fig. 2C) and *Hainosaurus bernardi* (Lingham-Soliar, 1992:fig. 6) is very different from state 0 in *Platecarpus* and *Plioplatecarpus*: the prefrontal overlaps the postorbitofrontal ventrally with a thin flange. State 1 was created to reflect this fundamental difference.

(28) [32] Postorbitofrontal shape: narrow (0); or wide (1).

(29) [33] Postorbitofrontal transverse dorsal ridge: absent (0); or present (1). Bell (1993) considered this ridge to be either a synapomorphy of Russellosaurina that reverses in *T. nepaeolicus* or a synapomorphy of Plioplatecarpini that is convergently autapomorphic

in his *Tylosaurus* taxon novum. While he coded it as missing for *T. proriger*, I can find no trace of this feature in any of the *Tylosaurus* species I have examined, and have coded it absent.

(30) [35] Maxillary tooth number: 20–24 (0); or 17–19 (1); or 15–16 (2); or 14 (3); or 13 (4); or 12 (5). *Tylosaurus proriger* and *T. nepaeolicus* can have either 12 or 13 teeth in maxilla, though 12 occurs more frequently in *T. nepaeolicus* and 13 more frequently in *T. proriger* (Russell, 1967:57). Since *T. pembinensis* (Chapter 2) and *H. bernardi* (Lingham-Soliar, 1992) also have 12–13 maxillary teeth, and *Taniwhasaurus oweni* (Caldwell et al., 2005) has 13–14, the character states have been coded using the maximum tooth count for these taxa.

(31) [36] Maxillo-premaxillary suture posterior terminus: suture ends above point anterior to or even with midline of fourth maxillary tooth (0); or between fourth and ninth teeth (1); or even with or posterior to ninth tooth (2).

(32) [37] Maxilla posterodorsal process: recurved wing of maxilla dorsolaterally overlapping portion of the anterior end of prefrontal (0); or process absent (1).

(33) [38] Maxilla posterodorsal extent: recurved wing of maxilla preventing emargination of prefrontal on dorsolateral edge of external naris (0), or not (1). It is clear from Bell's (1993:78, 1997:308) descriptions of this character that state 0 corresponds to the condition seen in *Tylosaurus*, *Ectenosaurus*, and *Plotosaurus*, making his coding in the matrix inverted but otherwise correct. Lingham-Soliar (1992) observed that the maxilla does not form the entire lateral margin of the external nares in *H. bernardi*, but several inconsistencies (see Chapter 2) lead me to code this character as missing until an exact determination can be made.

(34) [39] Jugal posteroventral angle: angle very obtuse or curvilinear (0); or slightly obtuse, near 120 degrees (1); or 90 degrees (2). A reconstruction of the skull of *H. bernardi* (Lingham-Soliar, 1992:fig. 3) shows a posteroventral angle of around 90 degrees, but figures of the holotype show that this angle is actually closer to state 1 (Lingham-Soliar, 1992:pl. 1).

(35) [40] Jugal posteroventral process: absent (0); or present (1).

(36) [41] Ectopterygoid contact with maxilla: present (0); or absent (1).

(37) [42] Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0); or teeth arise from thin pronounced vertical ridge (1).

(38) [43] Pterygoid teeth size: anterior teeth significantly smaller than marginal teeth (0); or anterior teeth large, approaching size of marginal teeth (1).

(39) [44] Quadrate suprastapedial process length: process short, ending at level well above mid-height (0); or of moderate length, ending very near mid-height (1); or long, ending distinctly below mid-height (2). The short suprastapedial process of *Hainosaurus bernardi* contrasts sharply with the moderate-length suprastapedial of *Taniwhasaurus oweni*, *Tylosaurus kansasensis* and *T. nepaeolicus*. Bell (1993, 1997) classified the quadrate of *T. proriger* as state 0, even though the suprastapedial ends very close to mid-height in this taxon, and so I have assigned the same state to *T. pembinensis* and *T. saskatchewanensis*. The differences between the 'short' suprastapedial of *T. proriger* and the 'short' suprastapedial of *Hainosaurus bernardi* are obvious, however, and a new definition of this character is probably warranted.

(40) [45] Quadrate suprastapedial process constriction: distinct, dorsal (0); or parallel-sided (1); or tapered (2). Bell's (1993, 1997) original character was binary. State 0

describes a suprastapedial process that is narrow at its dorsal origin, but expands distally; this morphology is typical of the Mosasaurinae (Russell, 1967:124). His second character state describes a suprastapedial process that lacks this constriction, which "results in an essentially parallel-sided process in posterodorsal view, but can also include the tapering form characteristic of some *Tylosaurus*" (Bell, 1997:308). This state thus encompassed two distinct morphologies: the parallel-sided suprastapedial typical of *Platecarpus* and *Plioplatecarpus*, and the tapered suprastapedial typical of *Tylosaurus*. Following Bell's (1997:310) suggestion that these two unconstricted morphologies have different origins, it seemed appropriate to split his second character state, lack of constriction, into two states that describe the suprastapedial more accurately. Bell (1993, 1997) assigned *Tylosaurus kansasensis* and *T. nepaeolicus* his second unconstricted state, but *T. proriger* was given state 0, and he did not explain this distinction. The suprastapedial process of *T. proriger* is relatively smaller than that of *T. nepaeolicus* in posterodorsal view, but has the same tapered profile, and so has also been assigned state 2. The extremely reduced suprastapedial process of *Hainosaurus bernardi* (Lingham-Soliar, 1992:fig. 9) is not described by any of these states, and has been coding as inapplicable.

(41) [46] Quadrate suprastapedial ridge: if present, ridge on ventromedial edge of suprastapedial process indistinct, straight and/or narrow (0); or ridge wide, broadly rounded, and curving downward, especially above stapedial pit (1).

(42) [47] Quadrate suprastapedial process fusion: no fusion present (0); or process fused to elaborated process from below (1).

(43) [48] Quadrate stapedial pit shape: pit broadly oval to almost circular (0); or relatively narrowly oval (1); or extremely elongate with a constricted middle (2).

(44) [49] Quadrate infrastapedial process: absent (0); or present (1).

(45) [50] Quadrate posteroventral ascending tympanic rim condition: small, low ridge present (0); or a high, elongate crest (1); or crest extremely produced laterally (2).

(46) [51] Quadrate ala thickness: ala thin (0); or thick (1).

(47) [52] Quadrate conch: ala and main shaft encompassing deeply bowled area (0); or alar concavity shallow (1).

(48) [53] Quadrate ala shape I: anterodorsal segment of tympanic rim more tightly curved than rest of rim (0); or rim with uniformly circular curve throughout (1).

(49) [54] Quadrate ala shape II: angular protuberance on anterodorsal edge of ala absent (0); or angular protuberance present (1).

(50) [55] Quadrate ala ridge: no vertical ridge present dorsolaterally on anterior face of ala (0); or strong obtuse ridge present in that position (1).

(51) [56] Quadrate ala groove: absent (0); or long distinct, and deep groove present in anterolateral edge of ala (1).

(52) [57] Quadrate tympanic rim size: large, almost as high as quadrate (0), or smaller, about 50-65% of the height (1).

(53) [58] Quadrate dorsal median ridge: relatively thin and high crest (0); or low, broadly, inflated dome (1).

(54) [59] Quadrate central median ridge: relatively thin and distinct (0); or in form of smooth broadly inflated dome around stapedial pit (1).

(55) [60] Quadrate ventral median ridge: single thin ridge (0); or thin ridge diverging ventrally (1). The median ridge is variably represented in different mosasaur genera. In *Tylosaurus* it forms the acuminate anteromedial edge of the quadrate, rather than facing directly medially as it does in most other mosasaurs, and so never achieves the derived condition of the previous two characters. The median ridge of *T. pembinensis* is bifurcated ventrally (Fig. 2-2B), but because the median ridge is well removed from the infrastapedial process on the posterior margin (Fig. 2-2C), it does not achieve the derived condition of this character.

(56) [61] Quadrate ventral condyle: condyle saddle-shaped, concave in anteroposterior view (0); or gently domed, convex in any view (1).

(57) [62] Quadrate ventral condyle shape: articular surface mediolaterally elongate (0); or very narrow and subtriangular or teardrop-shaped (1).

(58) [63] Quadrate ventral condyle modification: no upward deflection of anterior edge of condyle (0); or distinct deflection present (1).

(59) [64] Basisphenoid pterygoid process shape: process relatively narrow with articular surface facing mostly anterolaterally (0); or somewhat thinner, more fan-shaped with posterior extension of the articular surface causing more lateral orientation (1).

(60) [65] Basioccipital tubera size: short (0); or long (1).

(61) [66] Basioccipital tubera shape: tubera not anteroposteriorly elongate (0); or anteroposteriorly elongate with rugose ventrolateral surfaces.

(62) [67] Basioccipital canal: absent (0); or canal through basioccipital and basisphenoid present (1).

(63) [68] Dentary tooth number I: 20–24 (0); or 17–19 (1); or 15–16 (2); or 14 (3); or 13 (4); or 12 (5); or <12 (6). Lingham-Soliar (1992:178) observes that the type of *H. bernardi* bears 14 teeth in the dentary, but later gives the number in IRSNB 3672 as 13 (Lingham-Soliar, 1992:179). This discrepancy may stem from the fact that IRSNB 3672 has 12 maxillary teeth, while presumably the type has 13. The dentaries of *T. pembinensis* vary between 12 and 13 teeth (Chapter 2). As before, when tooth counts varied, coding was decided from the higher of the two numbers.

(64) [69] Dentary anterior projection: projection of bone anterior to first tooth present (0); or absent (1).

(65) [70] Dentary anterior projection length: short (0); or long (1).

(66) [71] Dentary medial parapet: parapet positioned at base of tooth roots (0); or elevated and straplike, enclosing about half of height of tooth attachment in shallow channel (1); or strap equal in height to lateral wall of bone (2).

(67) [72] Splenial-angular articulation shape: splenial articulation in posterior view almost circular (0); or laterally compressed (1); or intermediate (2).

(68) [73] Splenial-angular articular surface: essentially smooth concavo-convex surfaces (0); or distinct horizontal tongues and grooves present (1).

(69) [74] Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped (0); or very concave above, posterior wing greatly expanded (1).

(70) [75] Coronoid posteromedial process: small but present (0); or absent (1).

(71) [76] Coronoid medial wing: does not reach angular (0); or contacts angular (1).

(72) [77] Coronoid posterior wing: without medial crescentic pit (0); or with distinct excavation (1).

(73) [78] Surangular coronoid buttress: low, thick, about parallel to lower edge of mandible (0); or high, thin, rapidly rising anteriorly (1).

(74) [79] Surangular-articular suture position: behind condyle in lateral view (0); or at middle of glenoid on lateral edge (1).

(75) [80] Surangular-articular lateral suture trace: suture descending and angled or curved anteriorly (0); or virtually straight throughout length (1).

(76) [81] Articular retroarticular process inflection: moderate inflection, less than 60 degrees (0); or extreme inflection, almost 90 degrees (1).

(77) [82] Articular retroarticular process innervation foramina: no large foramina on lateral face of retroarticular process (0); or one to three large foramina present (1).

(78) [83] Tooth surface I: teeth finely striate medially (0); or not medially striate (1).

(79) [84] Tooth surface II: teeth not coarsely textured (0); or very coarsely ornamented with bumps and ridges (1).

(80) [85] Tooth facets: absent (0); or present (1).

(81) [86] Tooth fluting: absent (0); or present (1).

(82) [87] Tooth inflation I: crowns of posterior marginal teeth conical, tapering throughout (0); or crowns of posterior marginal teeth swollen near tip or above base (1).

(83) [88] Tooth carinae I: absent (0), or present but extremely weak (1); or strong and elevated (2).

(84) [89] Tooth carinae serration: absent (0); or present (1).

(85) [90] Tooth replacement mode: replacement teeth formed in shallow excavations (0), or in subdental crypts (1).

Postcranial Axial Skeleton

(86) [91] Atlas neural arch: notch in anterior border (0); or no notch in anterior border (1).

(87) [92] Atlas synapophysis: extremely redued (0); or large and elongate (1).

(88) [93] Zygosphenes and zygantra: absent (0); or present (1).

(89) [94] Zygosphenes and zygantra number: present on many vertebrae (0), present only on a few (1). Bell (1993, 1997) coded *T. nepaeolicus* as lacking zygosphenes and zygantra for the previous character, yet assigned it state 1 for this character. This seems counterintuitive, and since there is no record of *T. nepaeolicus* possessing these structures it has been coded as absent.

(90) [95] Hypapophyses: last hypapophysis occurring on or anterior to seventh vertebra (0); or on ninth or tenth vertebra (1).

(91) [96] Synapophysis height: facets for rib articulations tall and narrow on posterior cervical and anterior trunk vertebrae (0); or facets ovoid, shorter than centrum height on those vertebrae (1).

(92) [97] Synapophysis length: synapophysis of middle trunk vertebrae not laterally elongate (0); or distinctly laterally elongate (1).

(93) [98] Synapophysis ventral extension: synapophysis extending barely or not at all below ventral margin of cervical centrum (0); or some extending far below ventral margin of centrum (1).

(94) [99] Zygopophysis development: zygopophyses present far posteriorly on trunk vertebrae (0); or zygopophyses confined to anterior trunk series (1).

(95) [100] Vertebral body inclination: condyles of trunk vertebrae inclined (0); or condyles vertical (1).

(96) [101] Vertebral condyle shape I: condyles of anteriormost trunk vertebrae extremely dorsoventrally depressed (0); or slightly depressed (1); or essentially equidimensional (2).

(97) [102] Vertebral condyle shape II: condyles of posterior trunk vertebrae not higher than wide (0); or slightly compressed (1).

(98) [103] Vertebral synapophysis dorsal ridge: sharp ridge absent on posterior trunk synapophysis (0); or with sharp-edged and anteriorly precipitous ridge connecting distal synapophysis with prezygopophysis (1).

(99) [104] Vertebral length proportions: cervical vertebrae distinctly shorter than longest vertebrae (0); or almost equal or longest (1).

(100) [105] Presacral vertebrae number I: relatively few, 32 or less (0); or numerous, 39 or more (1). In mosasaurs the pelvic girdle has no attachment to the axial skeleton, but is presumed to have had a ligamentous attachment to the first pygal vertebra, which is distinct in possessing a synapophysis more than twice as long as that of the preceding dorsal (Williston, 1898:139; Russell, 1967:79). It is thus impossible to determine the beginning of the sacrum without a well-preserved vertebral column with intact synapophyses, and the presacral number is unknown for many taxa. In *T. pembinensis* the dorsal-pygal series cannot be differentiated (Chapter 2), and so this character is coded as unknown. In *T. saskatchewanensis* there are 43 vertebrae anterior to the first pygal (Chapter 3). Lingham-Soliar (1992) identified 40 presacral vertebrae in *H.*

bernardi, in contrast to Dollo's (1887:513) previous count of 49, but this does not affect the character coding.

(101) [106] Presacral vertebrae number II: if few, then 28 or 29 (0); or 30 or 31 (1).

(102) [107] Sacral vertebrae number: two (0); or less than two (1).

(103) [108] Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0); or several spines dorsally elongated behind middle of tail (1).

(104) [109] Hemal arch length: hemal arches about equal in length to neural arch of same vertebra (0); or length about 1.5 times greater than neural arch length (1).

(105) [110] Hemal arch articulation: arches articulating (0); or arches fused to centra (1).

(106) [111] Tail curvature: no structural downturn of the tail (0), or tail with decurved posterior portion (1).

(107) [112] Body proportions: head and trunk shorter than or about equal to tail length (0); or head and trunk longer than tail (1).

Appendicular skeleton

(108) [113] Scapula/coracoid size: both bones about equal (0); or scapula about half the size of coracoid (1).

(109) [114] Scapula width: no anteroposterior widening (0); or distinct fan-shaped widening (1); or extreme widening (2). Bell's two descriptions of this character are subtly different: at first state 2 is ascribed to an anterior border encompassing a half circle (1993:128), but later it is the distal margin that encompasses a half circle

(1997:317). Assuming that the later description is the most accurate, the scapulae of the two *Tylosaurus* species described in this thesis are best represented by state 2.

(110) [115] Scapula dorsal convexity: if scapula widened, dorsal margin very convex (0); or broadly convex (1).

(111) [116] Scapula posterior emargination: posterior border of bone gently concave (0); or deeply concave (1).

(112) [117] Scapula-coracoid fusion: ontogenetic fusion occurs (0); or no fusion at any life stage (1).

(113) [118] Scapula-coracoid suture: unfused scapula-coracoid contact has interdigitate suture anteriorly (0); or opposing surfaces without interdigitation (1).

(114) [119] Coracoid neck elongation: neck rapidly tapering from medial corners to relatively broad base (0); or neck gradually tapering to relatively narrow base (1).

(115) [120] Coracoid anterior emargination: present (0); or absent (1).

(116) [121] Humerus length: humerus distinctly elongate, about three or more times longer than distal width (0); or greatly shortened, about 1.5 to 2 times longer than distal width (1); or length and distal width virtually equal (2); or distal width slightly greater than length (3).

(117) [122] Humerus postglenoid process: absent or very small (0); or distinctly enlarged (1).

(118) [123] Humerus glenoid condyle: if present, condyle gently domed and elongate oval in proximal view (0); or condyle saddle-shaped, subtriangular in proximal view, and depressed (1); or condyle highly domed or protuberant and short ovoid to almost round in proximal view (2). Bell (1993, 1997) scored as absent all taxa whose condyles

were finished with cartilage, such as those of *Tylosaurus*, and this practice has been followed here.

(119) [125] Humerus pectoral crest: located anteriorly (0); or medially (1).

(120) [126] Humerus ectepicondylar groove: groove or foramen present on distolateral edge (0); or absent (1).

(121) [127] Humerus ectepicondyle: absent (0); or present as prominence (1). While very reduced ectepicondyles are present on the humeri of *T. pembinensis* and *T. saskatchewanensis* (Fig. 3-5A), they are not so prominent as the ectepicondyle of other mosasaurs, and so are coded as absent.

(122) [128] Humerus entepicondyle: absent (0); or present as a prominence (1). Here again the reduced entepicondyle typical of *Tylosaurus* is coded as absent.

(123) [129] Radius shape I: radius not expanded anterodistally (0); or slightly expanded (1); or broadly expanded (2).

(124) [130] Ulna contact with centrale: broad ulnare prevents contact (0), or ulna contacts centrale (1); or centrale not present as an ossification (2). A third character state was added to reflect the extreme reduction of the carpus in *Tylosaurus*: specimens which preserve a reasonably complete manus never show any trace of the centrale, or the intermedium of Russell (1967).

(125) [131] Radiale size: large and broad (0); or small to absent (1).

(126) [132] Carpal reduction: carpals number six or more (0); or five or less (1).

(127) [133] Pisiform: present (0); or absent (1).

(128) [134] Metacarpal I expansion: spindle-shaped, elongate (0); or broadly expanded (1).

(129) [135] Phalanx shape: phalanges elongate, spindle-shaped (0); or blocky, hourglass-shaped (1).

(130) [136] Ilium crest: blade-like, pointing posterodorsally (0); or elongate, cylindrical (1).

(131) [137] Ilium acetabular area: arcuate ridge supertending acetabulum (0); or acetabulum set into broad, short V-shaped notch (1).

(132) [138] Pubic tubercle condition: elongate protuberance located closer to midlength of shaft (0); or thin semicircular crest-like blade located close to acetabulum (1); or thin ala close to acetabulum (2). A third character state was added to reflect the reduced condition of the pubic tubercle for the species of *Tylosaurus* in which the pubis is described.

(133) [139] Ischiadic tubercle size: elongate (0); or short (1).

(134) [140] Astragalus: notched emargination for crural foramen, without pedunculate fibular articulation (0); or without notch, pedunculate fibular articulation present (1).

(135) [141] Appendicular epiphyses: formed from ossified cartilage (0); or from thick unossified cartilage (1); or epiphyses missing or extremely thin (2).

(136) [142] Hyperphalangy: absent (0); or present (1).

Chapter 4. General Discussion and Conclusions

This final chapter is intended to bring together the separate threads of the research chapters, and to consider their collective importance to the field of mosasaur research. In Chapter 2, the type and referred material of *Tylosaurus pembinensis* (Nicholls, 1988) is described, with many points of the anatomy of this species either corrected or clarified from the original description. The assignment of this species to *Hainosaurus* is rejected on the grounds that it possesses none of the anatomical features that have been demonstrated to belong to *Hainosaurus*, and the lack of a formal, functional diagnosis of this genus is established at length. In Chapter 3, the type material of the new species *Tylosaurus saskatchewanensis* is described from the Late Campanian Bearpaw Shale of Saskatchewan. Though this new taxon possesses some features typical of *Hainosaurus*, it also resembles *Tylosaurus*, and without a formal diagnosis of *Hainosaurus* it is referred to *Tylosaurus*. In Chapter 4, the cladistic matrix of Bell (1993, 1997) is reviewed with a focus on the tylosaurines, and some new tylosaurine taxa are added. The analysis of this expanded data set produces results consistent with previous studies, and provides the first tentative phylogeny of the tylosaurines.

This thesis and its conclusions are but a small facet of the lengthy taxonomic history of *Tylosaurus*. The profusion of early names generated by E. D. Cope and O. C. Marsh have been reduced to only two species, but the recent recognition of *T. kansasensis* (Everhart, 2005) means that there were three distinct species of *Tylosaurus* in the Niobrara Formation. The addition of another two species, one contemporaneous with the youngest occurrences of *T. proriger* in the Pierre Shale of South Dakota, and another representing the youngest record of the genus, makes *Tylosaurus* an extremely speciose genus amongst mosasaurs. Certainly there are no other genera for which so many species are represented by such complete material, and so *Tylosaurus* provides us a unique opportunity to investigate a group of related mosasaur species over time.

The two new species described in this thesis do not significantly expand our knowledge of *Tylosaurus* anatomy in general, but only because *T. proriger* has been so well described in the many publications on Kansas mosasaurs (Williston, 1898; Osborn, 1899; Russell, 1967). They present a variety of novel autapomorphies, such as the morphology of the frontal in *T. saskatchewanensis*, but are otherwise very similar to each other in terms of the general morphology of the bones and their contacts (Fig. 5-1). Though many anatomical details of *T. nepaeolicus* and *T. kansasensis* remain undescribed, it is possible to characterise some of the major anatomical themes within the genus. Exclusion of the prefrontal from the external narial margin by a process of the maxilla is common to all *Tylosaurus* species, and possibly also to *Hainosaurus* (see discussion of this character in Chapter 2). The prefrontal and postorbitofrontal are in contact above the orbit, and in younger species there is overlap of these two elements. The suprastapedial process of the quadrate is of moderate length, never contacting the infrastapedial process, and is tapered in outline; the infrastapedial varies in size and its relationship with the tympanic rim (Fig. 5-2). The marginal dentition is robust, with unequal lingual and buccal faces separated by a weak carina, and crown enamel is gently facetted with faint vertical striations at the base. Other important diagnostic features include the shape of the premaxillary rostrum, the length and position of the external naris, the area of muscular insertion on the posterior parietal table, and the position of the parietal foramen.

Though no other tylosaurine species is known so completely as those of *Tylosaurus*, we may also make some general comparisons of tylosaurine anatomy. The skulls of tylosaurine mosasaurs are conservative in structure (Fig. 5-1). The edentulous rostrum of the premaxilla and dentary remains their most distinctive feature. The prefrontal and postorbitofrontal contact and often overlap above the orbit. Tooth crowns are gently facetted, with faint vertical striations at the base, but may have strong to weak carinae and symmetrical to asymmetrical crowns. The quadrate is variable in the development of suprastapedial and infrastapedial process and tympanic ala, though the known examples of *Taniwhasaurus* and *Hainosaurus* are not well preserved and may be misleading (Fig. 5-2). The appendicular skeleton is poorly ossified, many elements having unfinished borders or extremities. The scapula is about one half the area of the coracoid. The femur and humerus are elongate, in length to width ratio rather than absolute length, with weak processes and poorly differentiated articular facets. In the carpus and tarsus the radiale, intermedium, pisiform, calcaneum, and second and third distal carpals are not ossified.

The phylogenetic tree (Chapter 4) resulting from a revision of Bell's (1997) data set does not differ substantially from previous findings, but does provide the first tylosaurine phylogeny. The character transformations supporting the monophyly of Tylosaurinae (see Chapter 4) are neither novel nor unexpected, being mostly a restatement of pre-cladistic systematics (eg. Williston, 1898; Russell, 1967). Synapomorphies within the Tylosaurinae are few in number, perhaps reflecting the missing data for *Taniwhasaurus* and *Hainosaurus*, resulting in poor support for that part of the tree. A basal position for *Taniwhasaurus oweni* within the Tylosaurinae has been suggested (Caldwell et al., 2005), but it was assumed that *Hainosaurus* would nest somewhere within the species of *Tylosaurus* (Bell, 1997:321). Instead, the phylogenetic tree shows a basal position for both of these taxa, though this position is not strongly supported. Prefrontal contribution to the narial margin is indicated as an important synapomorphy of *Tylosaurus*; this is corroborated by the two species in this thesis, but cannot be accepted pending confirmation of its absence in *Hainosaurus*.

Between the Late Coniacian and Late Campanian, the species of *Tylosaurus* have been part of varied vertebrate faunas in varied depositional settings. The geological occurrences of *T. pembinensis* and *T. saskatchewanensis*—dark, organic-rich, fine-grained clastics containing bentonite seams and diagenetic gypsum crystals—are nearly identical to that of *T. proriger* in the Sharon Springs Member of the Pierre Shale. *T. proriger* survived a profound shift in depositional environments, marked by the transition from chalks of the Niobrara Formation into overlying shales of the Pierre Shale, that surely represented substantial changes in water conditions throughout much of the seaway (Russell, 1993). On a larger scale than the local stratigraphy observed in the Mooreville Chalk (Wright, 1986), environmental conditions do not appear to be a strong control on the distribution of mosasaurs because of their active, nektonic habit (Nicholls and Russell, 1990). The differences in faunal composition between the occurrences of *Tylosaurus* species must thus be explained by some other factor.

The vertebrate faunas of the Niobrara Chalk and Sharon Springs and Pembina Members of the Pierre Shale have been described in considerable detail by Nicholls and Russell (1990) and Russell (1993). This encompasses all the known occurrences of *Tylosaurus* save for *T. saskatchewanensis* in the Bearpaw Shale of Saskatchewan. The fauna of this unit has never been described, or studied, in much detail. Russell (1993) reported the presence of *Plioplatecarpus* sp. and *Mosasaurus* sp., and this has been confirmed by recent expeditions to the area by the Royal Saskatchewan Museum and University of Alberta, but we still have no inventory of the relative abundance of these species. In terms of general faunal composition, however, the presence of *T. saskatchewanensis* in this fauna makes *Tylosaurus* the only genus to survive Russell's (1993) Niobrara "Age" and pass into the younger Navesinkan "Age." Although there is no great lithological difference between the Pierre Shale and Bearpaw Shale, their mosasaur faunas are profoundly different. The disappearance of many marine vertebrates, such as the fishes *Protosphyraena* and *Xiphactinus* and the mosasaurs *Platecarpus* and *Clidastes*, at the end of the Niobrara "Age" suggests that an important biological event occurred in the middle to late Campanian, independent of the environmental conditions evidenced by lithologies. Russell (1993) has suggested that this extinction was caused by the Manson impact event, a large impact structure in northwestern Iowa from which ejecta have been found in the Pierre Shale of South Dakota (Izett et al., 1993).

The anatomies of *T. pembinensis* (Chapter 2) and *T. saskatchewanensis* (Chapter 3) are now understood as completely as those of *T. proriger* and *T. nepaeolicus*, and in few respects considerably better. There are still many data missing from *Hainosaurus*, which has never been completely described, and *Taniwhasaurus*, for which many elements of the skull and postcranium remain unknown. Several species represented by incomplete material have been referred to the Tylosaurinae, such as *T. capensis* Broom and *M. gaudryi* Thévenin, but the information presented here provides no new insights into their identity. In terms of the progress of tylosaurine systematics, this thesis has actually forced us to take a step backward, by demonstrating that much of what Nicholls (1988) and Lingham-Soliar (1992) stated with confidence remains unknown or uncertain. Without a solid reference point for *Hainosaurus*, my taxonomic assignment of these two species fluctuated between *Tylosaurus* and *Hainosaurus* through the course of my thesis research, and their future remains uncertain. A comprehensive description of *H. bernardi* should allow for the creation of a formal diagnosis of *Hainosaurus*, and the removal of this uncertainty. This investigation is the most important avenue of future research identified in this thesis. Our current lack of a diagnosis of *Hainosaurus* is a stumbling block that prevents continued progress in tylosaurine systematics.

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FIGURE 5-1. Skulls of the tylosaurine mosasaurs discussed in this thesis. **A**, *Tylosaurus nepaeolicus* (after Russell, 1967). **B**, *Tylosaurus pembinensis* (Chapter 2). **C**, *Tylosaurus saskatchewanensis* (Chapter 3). **D**, *Hainosaurus bernardi* (after Lingham-Soliar, 1992). Not to scale.

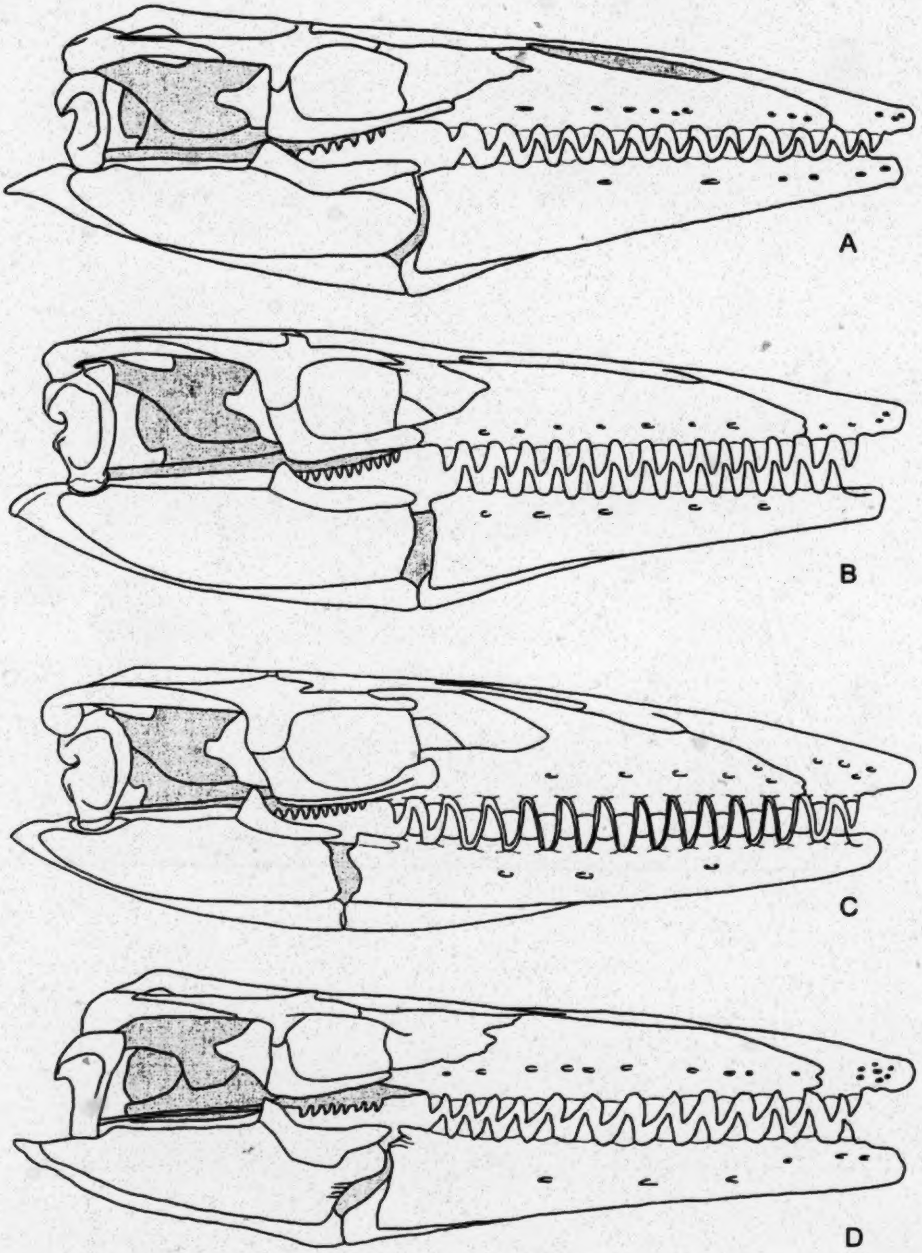

FIGURE 5-2. Quadrates of tylosaurine mosasaurs in left lateral view. **A,** *Tylosaurus kansasensis* (after FHSM VP 3366 from Everhart, 2005:fig. 3). **B,** *T. nepaeolicus* (after Russell, 1967:fig. 94). **C,** *T. proriger* (after Russell, 1967:fig. 94). **D,** *T. pembinensis* (Chapter 2). **E,** *T. saskatchewanensis* (Chapter 3). **F,** *Taniwhasaurus oweni* (after Caldwell et al., 2005:fig. 8). **G,** *Hainosaurus bernardi* (after IRSNB R23 and IRSNB 3672 from Lingham-Soliar, 1992:fig. 9). Not to scale.